SPATIAL AND TEMPORAL VARIABILITY IN RECRUITMENT TIMING, RELATIVE ABUNDANCE, AND MORTALITY OF JUVENILE RED DRUM (*SCIAENOPS OCELLATUS*) IN SOUTHEASTERN NORTH CAROLINA

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ABSTRACT

For many estuarine dependent fishes with protracted spawning periods, there is growing evidence that processes occurring during the juvenile life stage contribute to shaping year-class strength. Juvenile red drum, *Sciaenops ocellatus*, were collected from the New River and the Cape Fear estuaries continuously from estuarine arrival through age one using 18.3, 30.5, 60.1m seines, as well as multi-panel gillnets over a two year period. The relative abundance of age-0 red drum peaked in mid to late fall each year, and fish were present in shallow habitats into December before presumably moving to deeper waters during winter. Reappearance in shallow water habitats during spring was abrupt and occurred between late March and late April depending on spring warming rates. Red drum were consistently present in shallow areas until the next fall and were captured routinely in seines (through June) and gillnets (into September). Relative abundance of age-0 red drum was markedly higher throughout the entire first year of life in the New River compared to the Cape Fear River during the single year when both systems were sampled. Analysis of previous hydrodynamic research completed in each system suggests that differences in flow dynamics and flushing rates may play a role in the delivery of early juvenile red drum to these systems. Ages estimated from sectioned sagittal otoliths were used to backcalculate hatch date distributions and calculate daily instantaneous mortality rates. Hatch date distributions indicated that red drum typically spawned from July to October in southeastern North Carolina. However, peak spawning in both systems was indicated to occur significantly earlier in August during 2004 compared to early September as observed in 2003, and may have been a result of warmer nearshore water temperatures during summer 2004. Instantaneous mortality coefficients (Z) for age-0 postsettlement red drum during the 2004 fall period were 0.030 (3.0%/d) in the New River and 0.016 (1.6%/d) in the Cape Fear River. Large differences

in relative abundance of juvenile red drum during fall combined with significant differences in mortality rates (higher in New River) between estuaries suggests the potential for density-dependent mortality to occur during the juvenile stage. Cohort-specific mortality rates illustrated a trend of lower mortality for earlier hatched red drum in both estuaries, however patterns were highly variable and non-significant. Discrete overwinter loss rates ranged from 35-63% between November and May suggest that year-class strength of red drum may be further regulated by overwinter mortality. The findings of this study suggest that a combination of both abiotic (temperature, salinity, and tidal currents) and biotic processes occurring during the post-settlement stage have the potential to significantly alter initial patterns of recruitment and subsequent year-class strength of red drum in North Carolina estuaries.

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LITERATURE REVIEW

Early life history of marine fishes

Nearly 100 years ago, Hjort (1914), recognized the importance of early life stages as a major factor contributing to annual variability in fish abundance. Both biotic and abiotic processes affecting fish during early life are thought to contribute to observed variation. Many fishes undergo habitat transitions during early life involving transport from oceanic spawning grounds to estuarine nursery areas. In order to reach these nursery habitats at the optimal time, size, and condition--fish larvae require appropriate currents, physiologically favorable environmental conditions, and adequate food resources. Because mortality during early life is so high, research on recruitment variability in fishes has historically focused on factors influencing survival during the early larval period (Hjort 1914; Houde 1987; Cushing 1990).

For open marine populations, recruitment can be defined as the addition of individuals to local populations following settlement from the pelagic larval phase to benthic habitats (Caley et al. 1996). In studies of reef fishes, variation in the structure of fish assemblages and the sizes of their component populations has been shown to be a consequence of recruitment success during the pelagic larval phase (Victor 1983; Doherty and Williams 1988; Doherty and Fowler 1994). Doherty's recruitment-limitation hypothesis (1981) states that the supply of planktonic larvae may often limit future population sizes. Caselle (1999) noted that, "in its broadest interpretation, the recruitment limitation model assumes that both recruitment and post-recruitment mortality are independent of the number of settled individuals (no density dependence) and that patterns of supply drive patterns of adult density."

Although debate continues on the relative importance of the larval stage in determining recruitment (Leggett and DeBlois 1994), there is growing evidence that processes occurring

during the juvenile post-settlement period contribute to shaping year-class success (Campana 1996; van der Veer 1986; Bradford 1992). Work on both temperate and tropical reef fishes suggests that year-class strength may often rely on both larval supply and post-settlement processes, with all pre-recruit stages contributing to some degree (Steele 1997; Shima 2001). Multiple processes may influence patterns of abundance as local populations are often regulated by both recruitment and post-settlement density-dependent mortality (Jones 1990). Empirical evidence indicating the existence of density-dependent mortality does not rule out the prospect of recruitment limitation in regulating population size, just as empirical evidence of recruitment limitation does not rule out the possibility of density-dependent mortality or emigration (Caley et al. 1996).

In non-reef fishes, numerous examples also suggest that the juvenile stage plays an important role in shaping year-class strength (Crecco et al. 1983; Wooster and Bailey 1989; Myers and Cadigan 1993). Smith (1985) noted that overall year-class strength may be severely impacted by variable survival during the juvenile stage of many Clupeids. The emergence of strong year-classes in marine fishes may not always be related to larval supply and settlement (Steele 1997, Fromentin et al. 2001). Variability in population size originating in the larval stage may be further attenuated by density-dependent mortality in the juvenile stage (Myers and Cadigan 1993). Using mathematical models, Warner and Hughes (1988) demonstrated that local populations of coral-reef fishes may be regulated, not just limited, by recruitment (i.e. recruitment is effectively density-dependent). While variation in the supply of recruits may initially limit a population, both density-independent fluctuations in recruitment and density-dependent effects on settled juveniles contribute to patterns in adult numbers (Jones 1990).

High and variable mortality experienced by post-settlement juveniles (age-0) and sub-adults (age 1-2) may also disrupt associations between larval supply and eventual recruitment to the adult stage. Abundance estimates of recently settled fish may not reflect year-class strength if mortality is density-dependent in the juvenile stage. The abundance of early juveniles may not be strongly correlated with recruitment to the adult stage, while the abundance of older juveniles and sub-adults may demonstrate a stronger association (Bradford 1992). It is important to determine the age and size at which abundance and mortality stabilize if juvenile abundance is to be used as an index of year-class strength. Houde (1987) concluded that density-independent processes in egg and larval stages may be a major determinant of year-class strength in many marine fishes, but it is also important to understand the role that density-dependent processes play in regulating marine fish populations.

While there is still much controversy as to whether or not density-dependent regulation occurs in all marine populations (Sale and Tolimieri 2000), there is ample evidence of its existence in reef fish populations (Forrester 1995; Steele 1997; Schmitt and Holbrook 1999). In addition, Myers and Cadigan (1993) have also found strong evidence of density-dependent mortality during the juvenile stages of several marine demersal fishes including cod, plaice, sole, and whiting. Density-dependent processes that can potentially influence fish populations during early life include: (1) increased competition for food resulting in starvation or reduced growth rates; (2) sibling cannibalism within annual cohorts if spawning is protracted or growth is highly variable; (3) prey switching by predators targeting abundant year-classes, resulting in disproportionate predation mortality on members of a strong year-class; and (4) Refuge limitation as a result of competition for suitable nursery grounds. All of these processes can potentially contribute to density-dependent mortality to varying degrees on both fine and coarse

spatial and temporal scales. Of course, other processes may also produce density-dependent feedback. For example, density-dependent growth can combine with size-dependent predation to produce a density-dependent source of mortality (Sogard 1997). Hixon and Webster (2002) highlight the importance of defining the spatial boundaries and structure of a population, the nature of the demographic rates, and the spatiotemporal scales over which a population operates if biologists are to apply the basic concepts of density-dependence to a given population.

Demographic rates during early life may also be influenced by the timing of recruitment events. Young temperate fishes produced during a protracted spawning period may experience differences in growth and survival related to birth date (Crecco and Savoy 1985). Earlier hatched fish may have an increased probability of survival, due to longer exposure to warm temperatures and a longer growing season that equates to a large body size prior to winter. For example, length differences in largemouth bass within a cohort have been found to result from interactions between time of hatching and subsequent growth (Goodgame and Miranda 1993). Advantages of larger body size include predator avoidance and more efficient utilization of food sources. Phillips et al. (1995) noted that individuals that grow large early have an advantage in initiating and maintaining a pisciverous diet and therefore demonstrate higher growth rates, higher condition, and lower mortality. Pine et al. (2000) found that early-hatched cohorts of largemouth bass had a clear advantage over late-hatched cohorts in their ability to forage on a wider variety of prey, making them more likely to contribute to the new year-class. Rice et al. (1993) found that the vast majority of survivors of a cohort tended to be the fast-growing individuals, even after the majority of mortality had already taken place. Their findings also suggest that year-class strength may be set somewhat later in the early life history.

To identify the effects of size-selective mortality and growth at various stages in the early life history, back-calculated growth trajectories may be obtained from otolith derived ages (Campana and Neilson 1985, Parma and Deriso 1990, Campana and Thorrold 2001). Campana (2001) concluded that otolith derived age information forms the basis for calculations of growth rate, mortality rate, and productivity, ranking it among the most influential of biological variables for assessing the productivity of fish populations. While other calcified structures (i.e. vertebrae, fin rays, scales, and opercula) have been used in the past, otoliths have been used to age fish over the broadest range of ages and species (Secor et al 1995; Campana 2001). Otolith growth is allometric and appears to be the least sensitive to changes in fish condition (Campana and Neilson 1985). Otoliths are also one of the few calcified structures in fish that are non-skeletal and that are not subject to resorption (Campana 2001). During periods of starvation, growth appears to be maintained even when somatic growth is nonexistent and previously deposited otolith material is not resorbed (Campana and Neilson 1985; Maillet and Checkley 1990).

Biological growth and deposition of calcium carbonate on the otolith are controlled by endogenous rhythmic processes with daily frequencies. Pannella (1971) noted that the presence of daily increments in otoliths (sagittal) provide both an accurate and precise method for determining the daily age of a fish. The presence of easily discernable daily increments in otoliths provides and exceptionally accurate method for age estimation of most larval and juvenile fishes (Campana and Neilson 1985). Daily increments have been used to calculate overall growth rates, natural mortality rates (cohort and site-specific), as well as hatch-date distribution for juvenile and larval fishes. Demographic data obtained from otolith analysis can

be used to further examine spatial and temporal patterns of growth and survival during the post-settlement period.

Red drum early life history, ecology, and fishery information

The red drum, *Sciaenops ocellatus,* is an estuarine-dependent species that is distributed in marine and estuarine waters of the western Atlantic Ocean from Virginia to southern Florida, and throughout the Gulf of Mexico (Mercer 1984; Pattilo et al. 1997). The red drum has historically supported commercial fisheries along the Atlantic coast and the Gulf of Mexico and remains a highly-sought-after recreational species. The red drum has been designated the state fish of North Carolina, with 10 of the 16 current world records coming from this state (NCDMF).

Red drum are capable of spawning from the onset of maturity until death (Wilson and Nieland 1994). A study comparing Gulf of Mexico fish to those in the south Atlantic (Murphy and Taylor 1990) found most males along the Gulf coast were mature after they reached a length of 400mm, while males along the Atlantic coast were mature after they had reached 350mm. Females were mature at 600mm and 550mm in the Gulf of Mexico and along the Atlantic coast, respectively. Most males were mature by age 1 or 2, with all males being mature by age 3. Females matured as early as age 3; with all females mature by age 6. In both studies (Murphy and Taylor 1990; Wilson and Nieland 1994), male red drum appeared to mature at a smaller size and an earlier age. Assuming a maximum age of about 50 years, red drum spawning populations may contain as many as 45 year-classes (Latour et al 2001).

Red drum are batch spawners, with a mean batch fecundity of 1.54 million ova, and a spawning frequency of 2-4 days over an 8-9 week spawning season (Wilson and Nieland 1994). In North Carolina, spawning occurs during the summer and early fall (Weinstein 1979; Mercer

1984). Spawning aggregations of adult red drum have been observed near ocean inlets and passes along the Atlantic and Gulf coasts (Pearson 1929; Rooker and Holt 1997). After eggs have hatched, Rooker et al. (1999) suggest that there may be a short oceanic-planktonic phase just prior to recruitment to the estuary. Pelagic eggs and larvae are transported by tidal currents from offshore spawning sites into shallow bays and estuaries (Pearson 1929; Holt et al 1989).

Once in the estuary, recently settled juveniles have been found to use a variety of habitats that include salt marsh edges, nonvegetated mud bottoms, oyster reefs, and seagrass meadows (Stunz, et al. 2002). Estuarine habitats are believed to act as juvenile nurseries, providing calm shallow waters, abundant food resources, and protection from predators (Holt et al. 1983; Rooker and Holt 1997; Rooker et al. 1998, Stunz et al. 2002). In areas where seagrass coverage is sparse, marsh edges have been found to serve as important habitats for post-larval and juvenile red drum (Stunz et al. 2002).

During their first year, juvenile red drum demonstrate rapid growth both in length and weight (Rooker et al 1999; Scharf 2000). Vaughan and Carmichael (2000) estimated von Bertalanffy growth parameters for sub-adult and adult red drum in the coastal waters from North Carolina to Maryland (northern population) and the coastal waters from South Carolina to the Atlantic coast of Florida (southern population). Parameter values were estimated to be: L_{∞}=47.4, k=0.15, t_0=-2.15 (for red drum in the northern region); and L_{∞}=41.8, k=0.24, t_0=-0.72 (for red drum in the southern region). Negative t_0 estimates and relatively high rates of k suggest that red drum throughout the Atlantic experience rapid growth throughout much of their early life stages, followed by slower growth as they mature. Rapid growth in the early juvenile stage is thought to promote higher survival and early recruitment to the fishery. Estuarine areas that maximize

growth while minimizing mortality during the first year may be critical to year-class formation (Rooker and Holt 1997).

Juvenile and sub-adult red drum are believed to remain in estuaries for up to 3 to 4 years before moving to offshore habitats (Rooker et al. 1999; Scharf 2000; Denson et al. 2002; Collins et al. 2002). Young-of-the-year red drum are thought to move in and out of backwater areas and bays as they grow during the first year (Pearson 1928; Peters and McMichael 1997). Earlier studies suggest that juvenile red drum experience rapid growth during the summer and fall, followed by slower growth during winter months (Pearson 1929; Peters and McMichael 1987; Scharf 2000). Dietary shifts from small bottom invertebrates (amphipods, copepods and mysid shrimp) to larger decapods (blue crabs and penaeid shrimp) and fish (spot, croaker, menhaden), as well as increased metabolic rates associated with increasing water temperatures have been attributed to the exponential growth experienced by juvenile red drum in the spring (Boothby and Avault 1971; Bass and Avault 1975). Changes in water temperature also play a role in the spatial distribution of juvenile red drum. Juvenile fish have been noted to move into the deeper parts of estuaries and bays throughout Texas during the winter months (Pearson 1929, Scharf 2000). As water temperatures rise in the spring, juvenile red drum are thought to move back to shallow water habitats (Person 1929; Mercer 1984; Peters and McMichael 1997). However, the winter movement of juvenile red drum from shallow to deep waters throughout parts of the Gulf of Mexico is mostly speculative. It is based primarily on the absence of age-0 red drum in shallow water seine surveys during winter months followed by their return to these habitats in the spring. No data exists to document the presence of fish in deep-water locations, as trawl surveys during the winter have not captured fish consistently (Scharf 2000).

Overexploitation of red drum in many states has resulted in the closure of commercial fisheries and strict regulations have been implemented on recreational anglers to reduce growth and recruitment over-fishing. Currently, federal waters in the Atlantic are closed to the commercial harvest and possession of red drum. North Carolina is the only Atlantic state that still has a commercial fishery for red drum. The North Carolina Division of Marine Fisheries (NCDMF) has set an annual commercial quota of 250,000 lbs., a daily trip limit of 7 fish per day, and a slot limit requiring fish to be between 18-27 inches. The commercial fishery for red drum is by-catch only and red drum cannot make up greater than 50% of an individual's daily catch. Recreational fishermen are limited to one fish per day within the 18-27 inch slot. Other Atlantic states have also incorporated various slot limits and bag limits (Vaughan and Carmichael 2000). In Virginia, anglers are limited to 5 fish a day with a minimal total length of 18 inches, with one fish allowed to be greater than 27 inches. South Carolina and Georgia have incorporated a 5 fish per day limit and a slot limit requiring fish to be 14-27 inches. In Florida, anglers are limited to one fish per day and a slot limit requiring fish to be 18-27 inches.

The most recent assessments conducted by NCDMF conclude that red drum are "overfished", citing increased fishing pressure and the loss of essential estuarine habitats as areas of key concern (NCDMF 2001). In a recent stock assessment of red drum along the entire Atlantic coast, Vaughan and Carmichael (2000) calculated natural mortality (M) of subadults (ages 1 to 5) at 0.20 for the northern region (North Carolina to Maryland) and 0.23 for the southern region (South Carolina to Florida). For adults (ages 6 and older), the estimate of M was 0.12 for the northern region and 0.13 for the southern region. While natural mortality estimates have been calculated for sub-adult and adult red drum throughout various regions in the Atlantic

and the Gulf of Mexico, there is still a growing need for juvenile estimates of natural mortality and growth in North Carolina waters.

Currently, the NCDMF constructs a Juvenile Abundance Index (JAI) based on surveys completed each year for red drum throughout the state during the peak fall recruitment period (September through November). Since red drum may experience variable mortality throughout much of their early life history (Rooker et al. 1999), these surveys may not provide an accurate representation of year class strength. The age and size at which abundance and mortality stabilizes must first be established before the JAI can be used to accurately estimate year class success. This is especially true if mortality is density-dependent during the fall and winter. A previous study (Scharf 2000) conducted in Texas found that year-class strength of red drum may not be strongly correlated to the supply of early age-0 juveniles. Relationships between abundance estimates of age-0 fish and those for later life stages need to be closely examined to determine the most appropriate time in the life history to assess cohort success.

The South Atlantic Fisheries Management Council's Red Drum Fishery Management Plan (SAFMC 1990) has identified several areas for research in order to improve the management of red drum. Improved estimates of adult spawning stock biomass and adult abundance are needed. Better estimates of juvenile and sub-adult abundances are also needed to understand the long-term effects of management regulations on recruitment. Additional data is also needed from both the commercial and recreational fisheries to better estimate standing stock biomass and age composition of the catch. Additional demographic data for juvenile red drum is needed to fill any gaps that may exist in the NCDMF's current JAI program to index juvenile recruitment. Specifically, patterns of abundance, growth, and mortality of juvenile and sub-adult

red drum (age-0 and age-1) in North Carolina are needed to improve our understanding of processes that shape year-class strength.

With better estimates of adult and juvenile red drum abundance and the preservation of critical nursery habitats, management measures can be incorporated to improve the recreational and commercial fisheries, while at the same time ensuring the future viability of red drum populations. According to the guidelines outlined in the plan approved by the SAFMC, a minimum threshold of 30% Spawning Potential Ratio (SPR) has been set, with a target level of 40% SPR. Although, SPR estimates have increased from 1.3% to 18% in the north and 0.5% to 15% in the southern region, they have not been restored to the target level of 40% SPR. Current management strategies appear to be working to some extent, but more data is still needed before current management strategies can be fully evaluated.

INTRODUCTION

Year-class strength in marine fishes is believed to be to be the result of multiple processes that often interact. Many species demonstrate a bipartite life history strategy that includes a pelagic larval stage followed by a demersal juvenile stage. Although the initial number of larval recruits may shape broad patterns of abundance from year to year (Leggett and DeBlois 1994), high and variable mortality occurring after settlement to demersal habitats may disrupt associations between larval supply and eventual recruitment to the adult stage (van der Veer 1986; Jones 1990; Bradford 1992; Bailey 1994; Forrester 1995; Steel 1997). Often the abundance of juvenile fishes can be determined by both larval supply and post-settlement mortality (Houde 1987, 1989; Cushing 1990; Walters and Juanes 1993; Myers and Cadigan 1993; Leggett and DeBlois 1994; Shima 2001). Historically, research on recruitment variability has focused on the early larval period (Hjort 1914; Houde 1987, 1989; Cushing and Horwood 1994; Leggett and Deblois 1994), while less attention has been focused on evaluating the effects of variable juvenile growth and mortality on eventual year-class strength. However, several recent studies (Myers and Cadigan 1993; Hixon et al. 2002) have begun to shed light on the potential importance of first-year processes in structuring year classes. Importantly, Bradford (1992) concluded that abundance in the early juvenile sage may not be strongly correlated with recruitment to the adult stage, while abundance of late-stage juveniles and sub-adults often demonstrates a stronger association with that of adults.

The application of otolith derived age information has proven to be a powerful tool for assessing growth, mortality, and the productivity of fish populations. The presence of discernable daily increments in otoliths provides an accurate method for age estimation of most larval and juvenile fishes (Campana and Neilson 1985). Enumeration of daily increments has

been used to back-calculate birth dates and estimate the effects of variation in birth timing as well as variation in settlement location on survival. For example, Powell et al. (2004) used daily increment counts to calculate weekly hatch date distributions and the overall growth and mortality rates of larval and juvenile spotted seatrout (*Cynoscion nebulosus*) in Florida Bay. Daily increment counts have also been used to show that variable cohort-specific growth and mortality may lead to shifts in the demographic structure, biomass, and year-class strength of the American shad (*Alosa sapidissima*) in the Pamunkey River, Virginia (Hoffman and Olney 2005). Pine et al. (2000) also used daily increment counts to determine that earlier-hatched cohorts of largemouth bass (*Micropterus salmoides*) have an advantage over late-hatched cohorts, and that recruitment may be set during the juvenile stage rather than larval stages.

The red drum, *Sciaenops ocellatus,* is an estuarine-dependent species that is distributed in marine and estuarine waters of the western Atlantic Ocean from Virginia to southern Florida, and throughout the Gulf of Mexico (Mercer 1984; Pattilo et al. 1997). Spawning occurs during the summer and early fall (Mercer 1984; Comyns et al. 1991), when aggregations of adult red drum have been observed near ocean inlets and passes along the Atlantic and Gulf coasts (Pearson 1929; Rooker and Holt 1997). After a brief oceanic-planktonic phase, larvae are transported by tidal currents from offshore spawning sites into shallow bays and estuaries (Pearson 1929; Holt et al 1989; Brown et al. 2004). Settlement initially occurs in structured benthic habitats close to inlets, with individuals dispersing to lower salinity habitats with age. Juvenile and sub-adult red drum are believed to remain in estuaries for up to 3 to 4 years before moving to offshore habitats (Rooker et al. 1999; Scharf 2000; Denson et al. 2002; Collins et al. 2002; Stunz et al. 2002).

The early life history of red drum has been well studied for populations in the Gulf of Mexico (Pearson 1929; Bass and Avault 1975; Peters and McMichael 1987; Shultz and Steen

1991; Wilson and Nieland 1994; Rooker and Holt 1997; Rooker et al. 1998; Scharf 2000). However, along the Atlantic coast, data is limited to South Carolina (Daniel 1998; Wenner 2000; Jenkins et al. 2004). In North Carolina, red drum support an important recreational fishery as well as a by-catch-only commercial fishery. Despite their social and economic importance, very little is known about the early life history of red drum in North Carolina waters.

North Carolina represents the northern most Atlantic state where consistent and extensive recruitment of age-0 juveniles has been observed. Therefore, it is especially important to study early life processes in this population in order to detect any potential latitudinal variation that may represent local adaptations. Since 1991, the North Carolina Division of Marine Fisheries (NCDMF) has conducted a Juvenile Abundance Index (JAI) based on surveys completed each year for red drum throughout the state during the peak fall recruitment period (September through November). Currently, NCDMF conducts the vast majority of its JAI sampling in the central (Pamlico Sound, and the Neuse River) and northern regions (Albemarle Sound) of the state, with only a limited number of sampling locations in the southern region, specifically the New River. There are no sites currently sampled in the Cape Fear River, a large estuarine system, with the potential of supporting a large population of red drum. While the data is limited, there is evidence that the Cape Fear estuary and its surrounding tidal creeks may serve as primary nursery habitats for post-larval and juvenile red drum (Weinstein 1979; Weinstein et al. 1980; Schwartz et al. 1981), as well as sub-adults (Thorpe 2001). Additionally, the JAI has not been validated to determine if it is capable of forecasting recruitment to the fishery.

Here we present results from two consecutive years of field sampling designed to assess timing of juvenile recruitment, relative abundance, birth date distributions, and mortality rates of age-0 red drum in two large estuarine systems in southeastern North Carolina. Sampling was

conducted over a large spatial area in each system to identify broad-scale distribution patterns and seasonal shifts in relative abundance. Sampling was conducted biweekly initially and then weekly to increase temporal resolution and allow the influence of birth date and body size on mortality during the fall to be examined. Spring and summer sampling of late stage juveniles and sub-adults was also conducted to assess reductions in relative abundance due to overwinter loss.

METHODS

Study systems and sampling locations

Sampling for red drum was conducted in both the Cape Fear River and the New River estuaries, located in the southeastern region of North Carolina (Figure 1). In each system, sampling stations were selected based on their orientation to the mouth of the estuary and their salinity profiles. Stations furthest upriver with salinities ranging from 5 ppt to 15 ppt were designated as oligohaline, stations with salinities ranging from 15 ppt to 25 ppt near the middle part of the river were designated as mesohaline, and all stations located in the lower estuary near the mouth of the river with salinities greater than 25 ppt were designated as polyhaline. Within each region, stations were selected in order to sample several types of habitat shown to be used by newly settled red drum including: marsh edge, oyster shell, and soft mud bottom habitats, while still allowing active sampling gears to be swept efficiently.

Sampling for the 2003 red drum cohort in the New River began in the fall of 2003 at ten stations as site selection was still being finalized. For the 2004 cohort, the number of stations was reduced to six in order to allow increased sampling frequency at each of these sites starting in January of 2004. In the Cape Fear River, exploratory sampling was initially conducted at 8 to 14 stations starting in September 2004. By November, six final sites were selected for the remainder of the study period.

Seine Sampling:

Seine samples were collected at each station, during October 2003 through July of 2004 in the New River. Weekly seine samples were collected at each of the stations during August through December 2004 and bi-weekly samples were collected during January through June of

2005 in the New River. In the Cape Fear River, weekly seine samples were collected during September through December 2004 and bi-weekly samples were collected during January through June of 2005. Sampling was completed using a 30.2m x 1.8m bag seine (6.0mm mesh in the wings and 3.0mm mesh in the bag) at each station using standardized deployment and retrieval methods. Samples were excluded if the lead line was found to be snagged or raised from the bottom. At each station, salinity, dissolved oxygen, and water temperature were recorded using a YSI 85 meter. All species captured (macro-invertebrates and vertebrates) were sorted, identified and sub-samples (n=50) measured for total length. All red drum captured were counted, measured and weighed, and preserved in 95% ethanol to avoid otolith dissolution during storage.

Capture efficiency can be defined as the product of encirclement efficiency as the net is set (which decreases for larger fish) and retention efficiency as the net is retrieved (which increases for larger fish) (Bayley and Herendeen 2000). In this study, we were concerned about the effects on gear efficiency of increasing red drum body size in the spring. We assessed encirclement efficiency as a function of seine size using separate bi-weekly sampling during the spring of 2005 in the New River. We compared the encirclement efficiencies of three seine sizes (18.3m, 30.5m, and 61.0m) at a subset of our sample locations. The 18.3m and 30.5m seines were set by using the same standardized deployment and retrieval protocols used during our regular sampling. Encirclement times of the 18.3m and 30.5m seines generally ranged between 2-3 minutes. A 6.1m skiff was used to deploy the 61.0m seine in a semicircular pattern; resulting in relatively short encirclement times (< 1 minute). Once set, the 61.0m seine was retrieved by hand. Samples were excluded if the lead line was found to be snagged or if encirclement times for the 60.1m seine exceeded more than 1 minute.

Summer gillnet sampling for late stage juveniles and subadults

As fish grow larger, gear avoidance increasingly biases relative abundance estimates, due to increased swimming speeds and increased fish sensory perception (Bayley and Herendeen 2000). Thus, to capture older, larger age-0 red drum (9-12 months of age, 200-400 mm TL); gillnetting was conducted during summer months at the same stations at which seining was conducted. In the New River, multipanel gillnets were fished biweekly from June through August of 2004 and 2005. In the Cape Fear River, gillnets were fished biweekly from July to September in 2004. Gillnets measured 45.7m in length and consisted of 6 separate panels, each 7.6m in length, with stretched mesh sizes ranging from 2.5cm to 15.2cm. To ensure that the gillnets were fished close to the bottom, each net was constructed with 30 lb. lead line and fished with anchors at each end. Gillnets were set within one hour of sunset and retrieved shortly after sunrise, for a soak time of approximately 12 hours. Generally, each overnight set was fished for the duration of one complete tidal cycle. Gillnets were set perpendicular to the shoreline, with the smallest mesh being set nearest to the beach. At each station, salinity, dissolved oxygen, and water temperature were recorded during deployment and retrieval. All fish in each gillnet were identified, counted, and measured in the field. All red drum captured were placed on ice until they could be returned to the laboratory for processing.

Otolith removal and preparation

Sagittal otoliths have been used in a number of age and growth studies for red drum (Peters and McMichael 1987; Beckman et. al 1988; Murphy and Taylor 1990; David et al. 1994; Ross et al. 1995; and Baltz et al 1998). Sagittal otoliths have also been used to validate the

formation of daily rings in laboratory-reared red drum (Peters and McMichael 1987). Although no considerable morphological variation between left and right otoliths has been documented for red drum, we used the left sagittal otolith exclusively, unless it was damaged, in which case the right sagittal otolith was used.

Otolith removal and preparation followed the techniques outlined in Secor et al. (1991), with some minor variations. Specifically, before otoliths were sectioned and polished, they were first fixed in an embedding medium (EMBed-812). Embedded otoliths were then secured to a cutting slide using thermoplastic glue (Crystal Bond). After locating the core using a dissecting microscope, the otoliths were then sectioned in the transverse plane using an Isomet low-speed saw. Otoliths sections (~1mm thick) were polished on both sides using a polishing machine and fine grit paper. After the core was located in each section, the otoliths were hand polished using 3.0 micron alumina polishing powder to remove imperfections.

Otolith microstructure analysis

Daily aging of red drum otoliths was completed using a light microscope (100-400X). Age (in days) was estimated by counting all daily growth increments from the core to the posterior margin (medial edge) of each otolith (Figure 2). Blind counts were made by two separate readers; if the two counts differed by more than 10%, the otoliths were read again. If the two counts still differed by >10%, the otolith was discarded from further analysis. If the counts differed by no more than 10%, both counts were averaged to estimate the fish's age. All daily counts were made directly through the microscope lens, allowing the reader more control of the light source and the focal plane.

Age validation and correction factor

Campana (2001) noted that aging error can result from processing error associated with the structure being examined (not all axes show a complete growth record) and interpretation error among readers. Aging error that affects both accuracy and precision can be quantified if replicate age readings can be made from an unbiased known-age reference collection (Gröger 1999; Campana 2001). Hatchery-reared red drum ranging in age from 49 to 93 days old were obtained from the South Carolina Department of Natural Resources red drum stock enhancement program. Known age otoliths were processed using the same techniques as those used for the wild red drum. Blind counts were made by two separate readers along the medial edge. To insure that the collection was aged as accurately as possible, counts that differed by >10 days were read again; counts that still differed by >10 days were excluded from the analysis. If the counts differed by no more than 10 days, both counts were averaged to estimate the fish's estimated age.

The relationship between the actual age of the hatchery-reared fish and the estimated age was generated and then used to correct ages estimated for wild fish. The relationship for red drum aged along the medial axis is shown in Figure 3. Estimated ages underestimated actual ages by 5 to 25% with error increasing with age. Fish < 40 days old did not require correction.

Data analysis:

CPUE data was examined qualitatively to identify broad spatial and temporal patterns, seine efficiency, and gillnet selectivity. Gillnet selectivity parameters were estimated from catches collected in multipanel gillnets with slightly different mesh sizes using Holt's (1963) indirect method of estimation:

$$\ln(C_2/C_1) = a + bL$$

where C_1 and C_2 = number caught per length group, and L = mid-point of length class. The selectivity factor (SF) for mesh sizes m_1 and m_2 was estimated as:

$$SF = -2a \big/ b(m_1 + m_2)$$

Optimum lengths for each mesh size were then estimated as:

$$L_{m1} = (SF) * m_1 \qquad \text{and} \qquad L_{m2} = (SF) * m_2$$

Selection curves were constructed using the relationship:

$$P = e^{-(L-L_{mn})^2/2SD^2}$$

where P = probability of capture at a given length L in a gillnet mesh size of m_n.

Hatch dates were back calculated by subtracting the estimated age (in days) from the date of collection. Hatch date distributions were compared among estuaries and years using Kolomogorov-Smirnov two sample distribution tests. Individual fish were assigned to specific cohorts (early and late) based on hatch dates. Mortality rates were calculated separately for each cohort to evaluate the influence of recruitment timing on survival.

Daily instantaneous mortality rates were calculated based on catch curve analysis using Ricker's (1975) model of exponential decline:

$$N_t = N_0 e^{-Zt}$$

where N_t = numbers at age t; N_0 = estimated numbers at hatching; Z = instantaneous mortality coefficient (d^{-1}), and t = otolith-derived age (days since hatching). This model assumes that once the members of a cohort have settled in an estuary, there is no emigration or immigration during the period in which mortality is being calculated. Most evidence suggests that this assumption is reasonable for juvenile red drum, which are believed to reside in the estuaries in which they

initially settle for a period of 2 to 3 years before returning to the open ocean to spawn (Pearson 1929; Peters and McMichael 1987; Ross et al. 1995; Rooker et al. 1999, Scharf 2000). Regressions were fit to abundance (ln (n+1)) at age data with slopes representing estimates of Z. Age-specific juvenile mortality rates were compared among systems using ANCOVA. The level of sampling in the fall of 2003 did not permit mortality to be estimated for the 2003 cohort, and thus no interannual comparisons could be made. Additionally, in each system, red drum CPUE in the fall (November) was compared to CPUE the following spring (May) to estimate winter loss rate (mortality + emigration).

RESULTS

Environmental conditions at sample locations

Mean daily water temperatures recorded at each site for the 2004 cohort in the New River and Cape Fear River estuaries exhibited similar temporal patterns of variability (Figure 4a and 4b). Average daily water temperatures ranged from 10.6 to 32.7ºC for the 2003 cohort and 9.1 to 30.9ºC for the 2004 cohort in the New River. The 2003 cohort in the New River appeared to experienced periodic cooling events through out the spring, were as the 2004 cohort experienced longer sustained periods of warming. However, water temperatures during the months of March through May were significantly higher (ANOVA, $F = 12.80$, $P = 0.001$) for the 2003 cohort (17.9-26.6ºC) compared to those observed for the 2004 cohort (11.6-24.3ºC). In the Cape Fear River, water temperatures ranged from 8.28 to 29.3ºC, and were marked by sporadic cooling events in the spring. Water temperatures recorded during the months of March through May in the Cape Fear (12.1-20.3ºC) were also significantly lower (ANOVA, $F = 18.27$, $P < 0.0001$) than those observed in the New River for both the 2003 and 2004 cohort.

Salinities ranged from 1.6 to 39.2 ppt. in the New River (Figure 4c) and 1.0 to 30.4 in the Cape Fear River (Figure 4d). Salinities of stations in proximity to the New River inlet were also higher than those recorded at stations located near the mouth of the Cape Fear River. In the Cape Fear River, salinities recorded at stations further upriver were also noticeably lower than those observed in the New River relative to their location to the inlet.

Relative abundance and distribution

In total, 908 juvenile age-0 red drum were collected in beach seine sampling in the New River estuary representing the 2003 and 2004 cohorts. In 2003, a total of 234 red drum larvae

were collected with the highest relative abundance of recruiting individuals observed in mid to late November (Figure 5). Although beach seine sampling did not begin early enough in 2003 to examine red drum recruitment timing, NCDMF sampling for the red drum JAI indicated that early juveniles first recruited to the sampling gear in mid September. In 2004, 671 red drum were collected, and early juveniles were first captured in mid to late August. The highest relative abundance was observed during late October and early November (Figure 5). In both years, fish were generally captured in shallow habitats until mid- December, before fish emigrated from these habitats with declining water temperature. Sizes of early juveniles in the fall ranged from 14 to 63mm TL for the 2003 cohort (Table 1) and 14 to 102mm TL for 2004 cohort (Table 2).

In the Cape Fear River estuary, 159 age-0 red drum (12-72mm TL) were collected in the fall of 2004 (Table 3). Early juveniles were first detected in mid to late August and the highest relative abundance was observed during late September and early October (Figure 5). Beach seines conducted in the spring failed to regularly capture larger age-0 sub-adult red drum in the Cape Fear River estuary. Only one juvenile red drum was caught in 23 seine hauls between March and May. Considerable differences in the relative abundance of age-0 red drum were observed among estuaries (Figure 5). On average, catch rates in the New River estuary were three to four times greater than those observed in the Cape Fear River estuary in the fall of 2004 (ANOVA, $F = 21.11$, $P < 0.0001$).

Post-winter juveniles returned to shallow habitats abruptly when estuarine water temperatures reached approximately 16ºC. This occurred as early as April (see Figure 4), where fish were caught regularly through May before size-based gear avoidance resulted in lower catches in June. Red drum size ranged from 93 to 235mm TL (2003 cohort) and 77 to 211mm

TL (2004 cohort) in the spring. By spring, most juveniles were distributed further upriver compared to more even distributions during the fall (Figure 6). Spring catch rates for the 2003 cohort in the upper part of the river were five to seven times greater than those observed in the lower part of the river. A similar trend was also observed in for the 2004 cohort, were catch rates in the upper part of the river (4.67 red drum/haul) were nine times greater than those in the lower river (0.50 red drum/haul).

Using multi-panel gill nets, a total of 334 age-0 sub-adult red drum were caught in the New River estuary from 2003 to 2004. Over the course of the 2003 summer gill netting season, 178 red drum were collected in 725 hours of soak time and 156 red drum were collected in 462 hours of soak time in 2004. Similar to spring seining, average capture rates in summer gillnets were higher in mesohaline regions compared to polyhaline regions (Figure 6). Gill net catch rates in the New River estuary were also eight to ten times as high as those observed in the Cape Fear River estuary in the summer of 2004.

Seine capture efficiency

A total of 42 age-0 juvenile red drum (69 to 208mm TL; mean TL = 132mm) were collected in the 30.5m beach seine and 34 age-0 juvenile red drum (75 to 249mm TL; mean TL = 141) were collected in the 61.0m beach seine. Capture rates and size distributions were nearly identical for both the 30.5 m and 61.0m seines up to a size of 160mm TL, after which a rapid decrease in capture rate was observed for the 30.5m seine (Figure 7). The 18.3m seine proved to be inefficient at capturing larger age-0 juvenile red drum, thus its size distributions are not shown. Over the course of the experiment, only 3 age-0 juvenile red drum (100 to 139 mm TL; mean TL = 117 mm) were collected using the 18.3m beach seine. Capture efficiency for the

30.5m beach seine (our standard gear) appeared to remain consistent through May for capturing larger age-0 juvenile red drum.

Gillnet mesh selectivity

Gillnet mesh panels were size-selective and also affected overall capture rates of larger juvenile and sub-adult red drum (Figure 8). Length-frequency distributions of red drum caught in multi-panel gillnets in the New River were nearly identical during the summers of 2004 and 2005. Only the 5.08cm and 7.62cm stretch meshes consistently captured red drum, with size ranges of 180-363 mm TL for the 5.08cm mesh and 220-426mm TL for the 7.62 cm mesh. The slopes and intercept of the regression of natural logarithms of catch ratios for each mesh panel (5.08 and 7.62cm) and fish lengths (midpoints) were statistically significant ($r^2 = 0.911$, $P < 0.003$). The optimum selection lengths increased from 228.30 to 342.46 mm for the 5.05 and 7.62cm mesh sizes. The probabilities of capture of red drum for the different mesh sizes are shown in Figure 9.

Length at age

Length-at-age relationships for age-0 juveniles during the fall were developed separately for each estuary in 2004 (Figure 10). In the New River estuary, 176 age-0 red drum (13-98mm TL) were examined; individual ages ranged from 24 to 115 days. In the Cape Fear River estuary, 140 age-0 red drum (21-65mm TL) were examined with estimated ages ranging from 25 to 126 days. A significant difference in length at age among estuaries was detected (ANCOVA, slopes, $F = 101.00$, $P < 0.001$), which indicated faster growth rates in the New River estuary (see Lanier and Scharf in prep for a more detailed examination of red drum growth patterns).

Hatch-date distribution

The distribution of hatch dates, back-calculated from age and date of capture, indicated a protracted spawning period (Figure 11). During 2003 in the New River, estimated hatch dates extended over a 99 d period ranging from July 11th to October 18th in 2003. However, 97% of the fish had estimated hatch dates during August and September. In 2004, estimated hatch-dates demonstrated a similar temporal pattern ranging between July 4 and October 18. However, peak spawning was observed in early August, rather than early September as observed in 2003. Thus, hatch date distributions differed significantly between years in the New River (Kolomogorov-Smirnov test, $P < 0.05$). In the Cape Fear River, estimated hatch dates during 2004 also indicated a protracted spawning period, but occurred over a shorter period (76 d) ranging from July 8 to September 23 (Figure 11). Similar to observations in the New River in 2004, peak spawning of Cape Fear red drum occurred in early August. However the long right-hand tail of estimated hatch dates in October detected in the New River was not evident in the Cape Fear River. Despite the lack of October hatch dates in the Cape Fear River, there was no significant difference between the hatch date distributions of the two estuaries in 2004 (Kolomogorov-Smirnov test, $0.25 < P < 0.05$).

Estimation of mortality

Instantaneous mortality coefficients (Z) for age-0 postsettlement red drum during the 2004 fall period were 0.030 (3.0%/d) in the New River and 0.016 (1.6%/d) in the Cape Fear (Figure 12). A significant difference was detected between estuaries in 2004 (ANCOVA, slopes, $F = 3.99$; $P < 0.05$). In the New River, postsettlement red drum became available to the gear at approximately 30 d of age. Peak relative abundance occurred at ages of 50-55 d, and then

declined for older ages. In the Cape Fear River, postsettlement red drum first recruited to the gear at approximately 25 d of age. Peak relative abundance occurred at ages of 30-35 d and then declined for older ages. Instantaneous mortality coefficients (Z) ranged from 0.029 (2.9%/d) for the early cohort to 0.046 (4.5%/d) for the late cohort in the New River (Figure 13). The mortality rates for early and late cohorts were both statistically significant (early, $P < 0.001$; late, $P = 0.044$), with the early cohort showing a trend for lower mortality. However, the effect of hatch timing on mortality was not statistically significant (ANCOVA, slopes, $F = 1.07$, $P > 0.25$). In the Cape Fear River during 2004, instantaneous mortality coefficients (Z) showed the same trend of lower mortality for the early cohort (0.010) compared to the late cohort to (0.018) (Figure 14). However, this trend was also not statistically significant (ANCOVA, slopes, $F = 1.00$, $P > 0.25$).

Estimation of overwinter loss

A substantial decline in capture rate of the 2003 cohort was detected in the New River between the months of November (a month with consistent catch rates, but before temperature-dependent emigration from shallow habitats had begun) and May (a time when water temperatures had warmed sufficiently to ensure re-entry of juvenile red drum into shallow water habitats) (Figure 15). Catch rates decreased from 9.38 red drum per haul in November to 6.08 red drum per haul in May of 2003, with a discrete loss rate of 35%. An even greater decline was observed for the 2004 cohort, with catch rates decreasing from 8.29 red drum per haul in November to 3.10 red drum/haul in May, a discrete loss rate of 63%.

DISCUSSION

Spatial and temporal patterns in relative abundance

Considerable variation in relative abundance of juvenile red drum was observed between the New River and Cape Fear River estuaries and between study years. Relative abundance of age-0 red drum throughout the first year of life was three to four times greater in the New River than the Cape Fear River. Furthermore, a substantial degree of interannual variability in relative abundance of age-0 red drum was evident in the New River estuary, with higher catch rates in 2004. The NCDMF annual red drum JAI survey also indicated a statewide increase in CPUE of age-0 red drum from 2003 to 2004 (Figure 16).

The reproductive success of many marine fishes is linked to the timed transport into or out of estuaries. Several factors such as the local hydrodynamics, temperature, salinity, stratification, turbidity, and riverine discharges are thought to influence the distribution and retention of estuarine-dependent marine fishes (Norcross and Shaw 1984). Strong spatial correlations in the abundance of age-0 red drum along the Gulf coast of Texas suggested that patterns of recruit-delivery are influenced by local nearshore wind-driven currents over a broad spatial scale (Scharf 2000). Using oceanographic models to simulate settlement patterns of red drum larvae, Brown et al. (2005) concluded that wind forcing and estuarine flushing rates and bathymetry combine to dictate spatial and temporal patterns of abundance in specific estuaries. These processes have been found to influence the spatiotemporal variation in the larval supply of several recreationally and commercially important fishes (Atlantic menhaden, spot, summer flounder, and southern flounder) entering the Beaufort Inlet, North Carolina, and its surrounding estuaries (Blanton et al., 1999; Churchill et al., 1999; Forward et al. 1999; Luettich et al., 1999).

Therefore, wind-induced estuarine circulation could potentially influence the distribution and retention of juvenile red drum in both the New River and the Cape Fear River estuaries.

Differences in the local hydrology between the New River and Cape Fear River estuaries may partly explain the disparate levels of abundance of juvenile red drum observed between estuaries. The Cape Fear River estuary has been described as a deep, narrow, partially mixed, moderately eutrophic estuary that is strongly tide-affected (Giese et al 1985; Ensign 2004). The Cape Fear River is also unique because it is the only major estuary in North Carolina that has a relatively free and direct water access to the ocean (Giese et al. 1985). The New River, on the other hand has been characterized as a broad, shallow, highly eutrophic estuary (Mallin et al. 1997). In a recent study using digital bathymetric data to calculate estuarine flushing time, the Cape Fear River was found to have a much higher freshwater inflow than the New River (Ensign 2004). Flushing times in the Cape Fear River (1-22 days) were also much shorter than those observed in the New River (8-187 days). Both rivers showed similar seasonal patterns in which longer flushing times generally occurred in the summer months (May-October). Longer flushing times in the New River coupled with extended flushing times during summer could promote higher larval retention and subsequent settlement in the estuary during peak red drum spawning (August-September). The lengthened flushing time of the New River is also thought to reduce the tidal exchange at the mouth of the estuary, while the Cape Fear River has a higher tidal exchange and more direct connection to the ocean (Ensign 2004). Differences in tidal flow could potentially account for the higher abundance of juvenile red drum in the New River observed in this study. Juvenile red drum also were evenly distributed along both the western and eastern edges of the New River. However, in the Cape Fear River, juvenile red drum where only found along the eastern side of the river. Exploratory beach seine sampling conducted at 5

sites along the western side of the river during the fall failed to catch juvenile red drum. Large across-channel variation in the subtidal flow passing through the Beaufort Inlet, North Carolina, was found to influence the up-estuary transport of the larvae (Churchill et al. 1999; Forward et al. 1999). Net inflow in the eastern and central regions of the Beaufort Inlet was correlated to large concentrations of larvae along the eastern side of the inlet, whereas the net outflow on the western side of the inlet tended to hinder transport. Weinstein et al. (1980) indicated that water tended to move upriver along the eastern shoals of the Caper Fear River and tended to demonstrate net flow out of the river along the western edge of the channel. Thus, the uneven distribution of juvenile red drum in the Cape Fear River that we observed may have resulted partly from across-channel variation in tidal flow.

As fish grow, their ecological and physiological requirements often change. Thus, fish often adopt life history strategies to maximize energy gains and / or reduce mortality risks. A temporal habitat shift in the relative abundance of age-0 red drum was detected in the New River estuary during both 2003 and 2004. Both beach seine and gillnet catch rates indicated that by spring, most juveniles were distributed further upriver compared to more even distributions observed during fall. A pronounced spatial trend in the distribution of older age-0 red drum was also observed in the Cape Fear River and in the New River to a lesser degree, indicating that as fish grew older and larger, their distributions shifted further upriver (Figure 17). These results parallel the findings of Peters and McMichael (1987) who noted that older juvenile red drum were found in greater number in low salinity tidal creeks far upstream from the ocean inlet in Tampa Bay. Yokel (1966) also observed that juvenile red drum were more common at low salinities, whereas adults preferred higher salinities. Laboratory results indicate that both temperature and salinity gradients within an estuary can influence the distribution, growth, and

survival of juvenile weakfish (Lankford and Targett 1994). Age-0 Atlantic croaker have also been shown to migrate to oligohaline waters during the fall and winter (Haven 1959). Lankford and Targett (1994) concluded that differences in salinity tolerances may act as a physiological barrier that limits the diversity and abundance of piscivorous marine fishes that prey upon juvenile weakfish in low salinity areas. In a recent review Sheaves (2001) demonstrated that a considerable number of studies have reported low abundances of large piscivorous predators in shallow estuarine habitats, increasing the value of these areas as nurseries for juvenile fishes (Blaber and Blaber 1980). In this study, summer gillnet catches in both the Cape Fear River and the New River also indicated that more potential predators (summer flounder, bluefish, Atlantic sharpnose shark, and spiny dogfish) of juvenile red drum were captured in polyhaline waters as compared to catches further upriver. Thus, juvenile red drum may undertake ontogenetic habitat shifts primarily to avoid predators, but may also realize a physiological advantage related to osmoregulatory ability or cold tolerance in low to moderated salinity habitats.

Recruitment timing

For many marine fishes with protracted spawning periods, recruitment timing can shape broad spatial and temporal patterns of abundance. Latitudinal differences among stocks may further modify patterns of settlement and compound the effects of density-independent and density-dependent processes. In Chesapeake Bay red drum were observed to spawn as early as July, with peak spawning occurring in late September and October (Mansueti 1960). However, in Tampa Bay, the timing of appearance of larval and juvenile red drum indicate that spawning occurs somewhat later, from mid August through mid November, with peak spawning occurring between late August and mid October (Peters and McMichael 1987). Red drum collected in the

Aransas estuary, Texas, indicated that spawning activity was relatively high and continuous from September through October (Rooker and Holt 1997). Hatch-date distributions suggest that red drum in both the New River and Cape Fear River estuaries spawn earlier and over a broader period (76-99d) than red drum in the Gulf of Mexico (64d) (Rooker and Holt 1997). Using gonadosomatic indices (GSI) and maturity stages, Ross et al. (1995) found that both male and female red drum collected in North Carolina waters had well-developed gonads and were capable of spawning by July and that peak spawning occurred in August and September in North Carolina. The differential spawning strategies of Atlantic coast and Gulf coast red drum may be directly related to disparities in water temperature associated with latitude and their effect on length of growing season for juveniles.

In addition to shaping latitudinal patterns of recruitment timing, water temperature may also contribute to interannual variation in recruitment timing in a given region. A significant difference in hatch-date distributions of juvenile red drum was detected in the New River between 2003 and 2004. Estimated hatch dates for the 2003 red drum cohort indicated that spawning took place from July through October, with peak spawning occurring in late August and early September. Peak spawning of the 2004 cohort occurred significantly earlier in –mid August. Hatch date distributions for the 2004 cohort in the Cape Fear River also indicated peak spawning occurred in early August. In the Gulf of Mexico, peak egg and larval abundances indicated that most red drum spawned when water temperatures over the shelf decreased rapidly from 27-29ºC to 24-25ºC (Comyns et al. 1991). Laboratory experiments have indicated that the optimum temperature for hatching was 25ºC and that high temperatures (30-35ºC) were associated with poor survival of yolk-sac larvae (Holt et al. 1981). Between June-August, mean nearshore water temperatures offshore of Hatteras Inlet, North Carolina, were significantly

higher (ANOVA: F = 42.88, P< 0.0001) in 2004 ($\bar{X}$ = 26.6ºC) than 2003 ($\bar{X}$ = 24.8ºC) (Figure 18). Water temperatures were also much higher in early August 2004 ($\bar{X}$ = 28.4ºC) than in late August 2003 ($\bar{X}$ = 26.5ºC). Using temperature as a cue, red drum may spawn earlier when conditions are optimum to increase the length of their growing season. Higher-than-average nearshore water temperatures observed in 2004 could account for interannual differences observed in the hatch date distributions of the 2004 cohort in the New River.

Size at age and mortality

Significant spatial differences in the growth and mortality rates of the 2004 cohort were observed between the New River and Cape Fear River estuaries. Fall growth rates of age-0 juvenile red drum in the New River (0.76mm/d) were significantly higher than those estimated for fish in the Cape Fear River (0.45mm/d). Laboratory experiments have indicated that temperature, salinity, and fish density can influence growth in young red drum (Holt et al. 1981; Lee et al. 1984; Smith and Fuiman 2003). The disparity in growth rates observed between estuaries in this study may be driven more by hydrological differences (temperature and salinity) and potential prey availability rather than density-dependent growth, given that both the growth rate and abundance of juvenile red drum were higher in the New River. While disparities in growth rates were evident among estuaries in this study, both rates were within the range of growth rates reported by Peters and McMichael (1987) in Tampa Bay, Florida (0.4 to 0.6mm/d), Rooker and Holt (1997) in Aransas Bay, Texas (0.41-0.58mm/d), Scharf (2000) along the Texas coast (0.6mm/d) and Stunz et al. (2002) in Galveston Bay, Texas (0.45mm/d). For a more detailed discussion of red drum growth see Lanier and Scharf (in prep).

There is growing evidence that the juvenile stage plays an important role in shaping year-class strength in marine fishes. Experimental studies of reef (Steele 1997; Shima 2001) and non-reef (Crecco et al. 1983, Smith 1985; Wooster and Bailey 1989; Myers and Cadigan 1993) fishes reveal the importance of processes that occur post-settlement in determining eventual cohort success. For many marine fishes, larval mortality rates are often much higher than those experienced by late stage juveniles (Cushing 1975). While high and variable mortality experienced during the early larval stages may shape initial patterns of local abundance, post-settlement density-dependent processes may play an important role in regulating marine fish populations. Cushing (1975) proposed that density-independent effects on year class abundance that occur during larval stages may be ultimately modulated by density-dependent processes during later life stages. Thus, relationships between the initial supply of recruits and subsequent year-class strength may be further attenuated by multiple processes that occur during the juvenile stage.

Considerable differences in the mortality rates of juvenile red drum were detected among estuaries. Estimated mortality during fall in the New River (3.0%/d) was nearly twice as high as mortality estimated in the Cape Fear River (1.6%/d) for age-0 juvenile red drum ranging in size from 20-100mm TL. Similar daily mortality rates (1-2%/d) were reported for juvenile fish (25-350mm TL) over a 9 month period along the Texas coast (Scharf 2000). Both the estimates of mortality reported in this study and those of Scharf (2000) are considerably lower than those reported for early post-settlement red drum (3-40mm TL) in the Gulf of Mexico (12.5%/d to 13.%/d) (Rooker et al. 1999). The results of this study and those of Scharf (2000) suggest as juvenile red drum grow larger, mortality stabilizes. Thus, abundance indexes of late stage juveniles may be a better indication of year-class strength.

If CPUE can be used as an index of relative density, links between high levels of variation in the relative abundance of juvenile red drum and overall differences in annual cohort mortality could potentially indicate if mortality is related to density in southeastern North Carolina. CPUE of age-0 red drum in the fall of 2004 was three to four times greater in the New River compared to the Cape Fear River. Estimated mortality during fall in the New River was twice as high as the Cape Fear River. These findings are suggestive of potential density-dependent mortality among early juveniles, but do not provide direct evidence of its existence. However, there is ample evidence that density-dependent mortality exist in reef fish populations (Forrester 1995; Steele 1997; Hixon and Webster 2002; Johnson 2006) as well as several marine demersal species (van der Veer 1986; Myers and Cadigan 1993; van der Veer et al. 2000; Fromentin et al. 2001). Thus, the effect of large year-classes of incoming recruits may be dampened by density-dependent processes in the estuary. Our findings represent indirect evidence that density-dependent processes during the juvenile life stage may contribute to year-class formation of red drum in North Carolina estuaries.

Fish with protracted spawning strategies often experience differences in growth and survival relating to hatch timing. Cohort-specific mortality rates indicated that early season cohorts (2.9%/d) experienced lower mortality rates compared to late season cohorts (4.5%/d) in the New River in 2004. A similar trend was also detected in the Cape Fear River that same year. This finding contrasts slightly with the results of Rooker et al. (1999), who concluded that mid season red drum cohorts in the Gulf of Mexico experienced lower mortality than early and late season cohorts due to differences in temperature and prey and predator densities. Latitudinal differences in temperature, salinity, and duration of spawning events may be responsible for regional differences in cohort-specific mortality of red drum. In addition, sample size prevented

us from separating annual cohorts into three sub-cohorts based on hatch timing, so comparisons are difficult. The potential disadvantages of late hatch timing have been illustrated in studies of other fishes. For example, juvenile mortality of American shad was found to increase throughout the season, resulting in declining biomass during the juvenile stage (Hoffman and Olney 2005). Also, early-hatched cohorts of largemouth bass were found to have clear size advantages throughout the growing season over late-hatched cohorts, increasing survivorship and likely contribution to the adult population (Pine et al. 2000). Longer growing seasons and exposure to warm temperatures may allow for faster growth and increase the probability of survival of young-of-the-year temperate fishes produced early during a protracted spawning period (Crecco and Savoy 1985).

Garvey et al. (1998) concluded that the overwinter survival and recruitment of age-0 largemouth bass may increase with improved first-summer growth resulting from earlier hatching. Earlier hatched largemouth bass were also found to forage on a broader prey base, resulting in enhanced lipid accumulation and increased survival over their first winter (Pine et al. 2000). Post and Evens (1989) concluded that overwinter mortality of YOY yellow perch was strongly size related and that smaller fish would be expected to have higher mortality as a result of low energy reserves and high metabolic rates. Being at the northern extent of their range, hatch timing may have additional effects on survival of age-0 red drum in North Carolina estuaries. Reduced body size resulting from late hatch timing coupled with extreme cold winter temperatures can lead to substantial overwinter losses. Osmoregulatory failure as a result of exposure to prolonged cold temperatures has been shown to influence the survival of other age-0 fishes including large mouth bass (Russell et al. 1998), white crappie (McCollum et al. 2003), Atlantic croaker (Lankford and Targett 2001), and summer flounder (Malloy and Targett 1991).

Consistent catches for fish up to 160mm TL in the 30.5m beach seine in November and May allowed CPUE to be compared to estimate overwinter loss (death + emigration) of age-0 red drum. In the New River estuary, discrete overwinter loss rates ranged from 35 to 63%, indicating that the first winter of life may have broad implications in determining year-class strength. Lankford and Targett (2001) concluded that temperature-mediated overwinter mortality may regulate the recruitment success and subsequent year-class strength of Atlantic croaker in some Mid-Atlantic Bight estuaries. Thus, year-class strength of red drum may be further regulated by overwinter mortality.

The findings of this study suggest that red drum year-class strength may be determined not only by the supply of settling recruits, but also by processes occurring during post-settlement stages in the estuary which may significantly modify initial patterns of recruitment. Bradford (1992) cautioned that the abundance of early juveniles may not be strongly correlated with recruitment to the eventual adult stage, while the abundance of older juveniles and sub-adults may demonstrate a stronger association with the number of adults. Thus, the need to validate the current methods used to forecast recruitment and year-class strength is clear. Given the substantial overwinter losses observed in the New River estuary, it is important to determine the age and size at which abundance and mortality stabilize if juvenile abundance is to be used as an index of year-class strength. Caution should also be used when using demographic data derived from otolith analyses, given the high degree of error surrounding the interpretations of daily increments. Based on the results presented in this paper, the development of a correction factor is necessary to ensure the accuracy of daily incremental counts of wild red drum. Given the invaluable demographic data provided from otolith microstructual analyses, greater steps should be taken to validate age estimation for each species. Successful predictions of future year-class

strength not only require an understanding of density-dependent and density-independent processes, but an understanding of the linkages between the juvenile stage and the eventual recruitment to the adult population. If their effects can be separated, future fisheries management plans and models will be able to better incorporate some of the mechanistic links between the dynamics of fish populations and climatic variability.

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Table 1. Weekly beach seine CPUE, mean TL, minimum TL, and maximum TL for the 2003 New River red drum cohort during the first year.

Date of capture	Red Drum	Seine Hauls	CPUE (#/haul)	Mean TL (mm)	SD TL (mm)	Minimum TL (mm)	Maximum TL (mm)
10/5/03	13	3	4.33	28.4	± 8.0	17.0	41.0
11/17/03	24	4	6.00	34.0	± 8.8	14.0	49.0
11/21/03	51	4	12.75	45.3	± 7.2	28.0	63.0
12/11/03	13	4	3.25	40.5	± 9.9	28.0	60.0
1/23/04	1	3	0.33	46.0	n/a	46.0	46.0
1/30/04	0	4	0.00	n/a	n/a	n/a	n/a
2/6/04	1	4	0.25	39.0	n/a	39.0	39.0
2/13/04	0	4	0.00	n/a	n/a	n/a	n/a
2/20/04	0	5	0.00	n/a	n/a	n/a	n/a
3/19/04	1	3	0.33	54.0	n/a	54.0	54.0
3/26/04	6	5	1.20	48.3	± 4.2	42.0	55.0
4/2/04	2	5	0.40	73.0	± 8.5	67.0	79.0
4/9/04	12	3	4.00	62.0	± 3.9	55.0	68.0
4/16/04	2	5	0.40	72.0	± 3.9	68.0	76.0
4/23/04	11	5	2.20	85.1	± 10.5	63.0	101.0
4/30/04	3	5	0.60	98.3	± 11.8	91.0	112.0
5/6/04	32	5	6.40	110.5	± 13.0	93.0	155.0
5/14/04	7	5	1.40	111.6	± 9.6	96.0	124.0
5/20/04	34	5	6.80	137.7	± 8.8	120.0	154.0
5/25/04	2	5	0.40	134.0	± 11.3	126.0	142.0
6/3/04	4	5	0.80	168.0	± 2.6	165.0	171.0
6/7/04	5	5	1.00	155.4	± 20.1	128.0	181.0
6/16/04	4	5	0.80	193.0	± 9.4	183.0	201.0
6/22/04	0	5	0.00	n/a	n/a	n/a	n/a
6/28/04	4	5	0.80	220.0	± 14.9	201.0	235.0
7/8/04	1	5	0.20	231.0	n/a	231.0	231.0
7/14/04	1	5	0.20	161.0	± n/a	161.0	161.0
7/20/04	0	5	0.00	n/a	n/a	n/a	n/a

Table 2. Weekly beach seine CPUE, mean TL, minimum TL, and maximum TL for the 2004 New River red drum cohort during the first year.

Date of capture	Red Drum	Seine Hauls	CPUE (#/haul)	Mean TL (mm)	SD TL (mm)	Minimum TL (mm)	Maximum TL (mm)
8/4/04	0	5	0.00	n/a	n/a	n/a	n/a
8/10/04	0	5	0.00	n/a	n/a	n/a	n/a
8/17/04	1	5	0.20	22.0	1.4	22.0	22.0
8/24/04	0	5	0.00	n/a	n/a	n/a	n/a
9/1/04	3	6	0.50	26.0	n/a	25.0	27.0
9/9/04	0	6	0.00	n/a	n/a	n/a	n/a
9/13/04	12	6	2.00	30.5	9.2	14.0	49.0
9/21/04	19	6	3.17	27.4	8.3	15.0	45.0
9/29/04	43	6	7.17	36.2	5.0	18.0	39.0
10/5/04	6	6	1.00	32.8	7.3	20.0	38.0
10/12/04	71	6	11.83	28.0	8.5	15.0	46.0
10/18/04	101	6	16.83	32.1	9.8	18.0	65.0
10/25/04	22	6	3.67	36.4	12.1	19.0	66.0
11/1/04	55	6	9.17	36.6	9.9	20.0	78.0
11/8/04	99	6	16.50	44.0	9.6	25.0	73.0
11/15/04	31	6	5.17	44.6	8.8	24.0	60.0
11/22/04	34	6	5.67	46.6	8.0	36.0	70.0
11/29/04	38	6	6.33	50.6	13.4	28.0	102.0
12/9/04	69	6	11.50	52.5	11.1	29.0	81.0
12/17/04	11	6	1.83	54.0	8.4	41.0	70.0
1/12/05	17	6	2.83	52.9	10.7	38.0	76.0
1/26/05	0	6	0.00	n/a	n/a	n/a	n/a
2/9/05	2	6	0.33	62.0	1.4	61.0	63.0
2/24/05	0	6	0.00	n/a	n/a	n/a	n/a
3/15/05	0	6	0.00	n/a	n/a	n/a	n/a
3/21/05	0	6	0.00	n/a	n/a	n/a	n/a
4/6/05	1	6	0.17	69.0	n/a	69.0	69.0
4/18/05	1	6	0.17	92.0	n/a	92.0	92.0
5/2/05	11	6	1.83	96.7	12.4	77.0	118.0
5/19/05	20	6	3.33	160.2	24.0	111.0	207.0
6/2/05	2	6	0.33	129.0	8.5	123.0	135.0
6/16/05	5	6	0.83	190.2	18.0	172.0	211.0

Table 3. Weekly beach seine CPUE, mean TL, minimum TL, and maximum TL for the 2004 Cape Fear River red drum cohort during the first year.

Date of capture	Red Drum	Seine Hauls	CPUE (#/haul)	Mean TL (mm)	SD TL (mm)	Minimum TL (mm)	Maximum TL (mm)
9/10/04	1	4	0.25	18.0	n/a	18.0	18.0
9/15/04	7	6	1.17	19.7	± 7.8	15.0	36.0
9/22/04	12	7	1.71	22.8	± 7.4	13.0	40.0
9/29/04	22	6	3.67	29.5	± 8.0	18.0	52.0
10/6/04	14	7	2.00	19.8	± 5.6	12.0	31.0
10/13/04	33	6	5.50	31.7	± 11.1	17.0	58.0
10/22/04	5	6	0.83	33.8	± 15.8	21.0	59.0
10/27/04	0	6	0.00	n/a	n/a	n/a	n/a
11/3/04	3	6	0.50	31.3	± 4.2	28.0	36.0
11/9/04	10	3	3.33	46.1	± 8.7	30.0	55.0
11/17/04	0	1	0.00	n/a	n/a	n/a	n/a
11/19/04	15	6	2.50	50.7	± 8.6	35.0	62.0
11/23/04	8	6	1.33	56.1	± 8.2	42.0	68.0
12/3/04	1	6	0.17	59.0	n/a	59.0	59.0
12/7/04	14	6	2.33	54.9	± 7.7	43.0	72.0
12/16/04	0	6	0.00	n/a	n/a	n/a	n/a
1/4/05	0	6	0.00	n/a	n/a	n/a	n/a
1/20/05	0	6	0.00	n/a	n/a	n/a	n/a
2/1/05	0	6	0.00	n/a	n/a	n/a	n/a
2/17/05	0	3	0.00	n/a	n/a	n/a	n/a
2/18/05	0	3	0.00	n/a	n/a	n/a	n/a
3/3/05	0	6	0.00	n/a	n/a	n/a	n/a
3/17/05	0	6	0.00	n/a	n/a	n/a	n/a
3/31/05	0	6	0.00	n/a	± 24.4	n/a	n/a
4/12/05	0	6	0.00	n/a	n/a	n/a	n/a
4/28/05	0	1	0.00	n/a	n/a	n/a	n/a
4/29/05	0	5	0.00	n/a	n/a	n/a	n/a
5/11/05	1	6	0.17	117.0	n/a	117.0	117.0
5/25/05	0	6	0.00	n/a	n/a	n/a	n/a
6/10/05	0	5	0.00	n/a	n/a	n/a	n/a
6/20/05	0	3	0.00	n/a	n/a	n/a	n/a
6/24/05	0	2	0.00	n/a	n/a	n/a	n/a

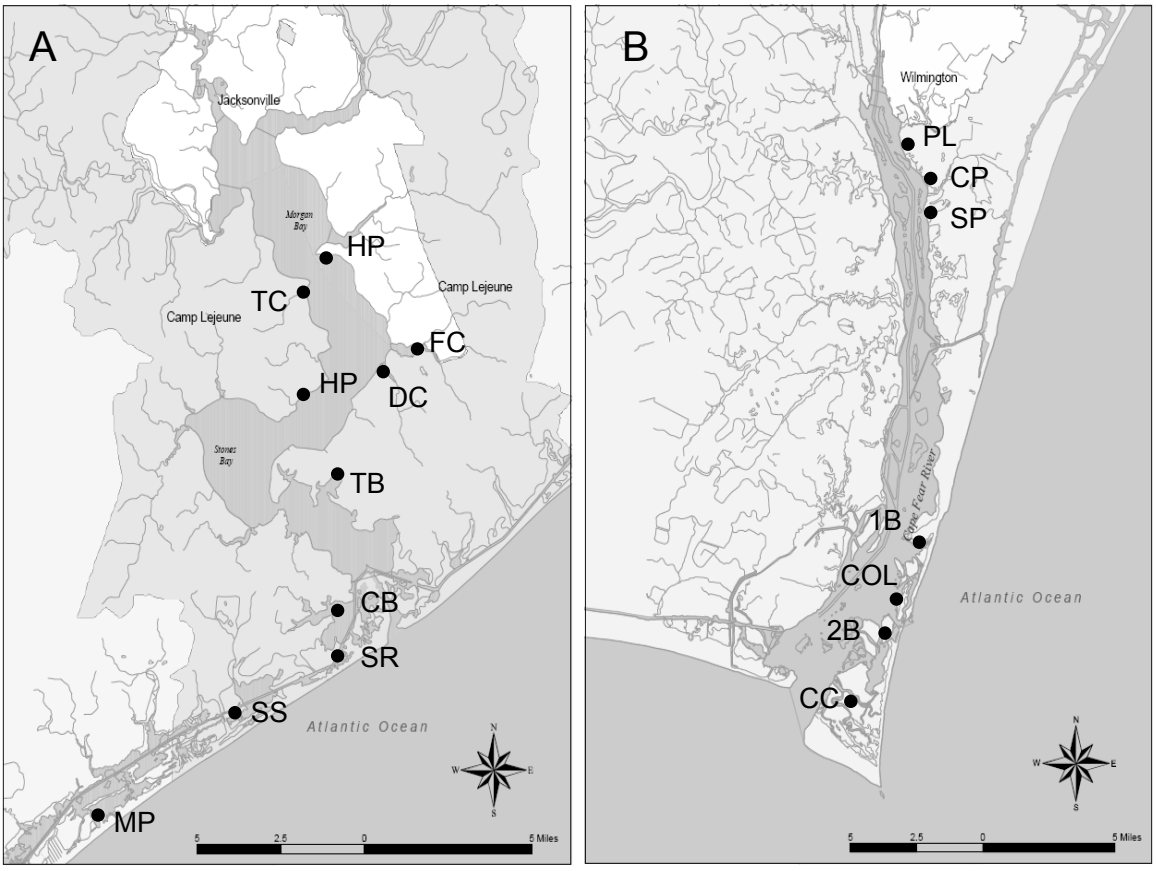

Figure 1. Locations of beach seine and gill net sample stations in the New River estuary (A) and Cape Fear River estuary (B).

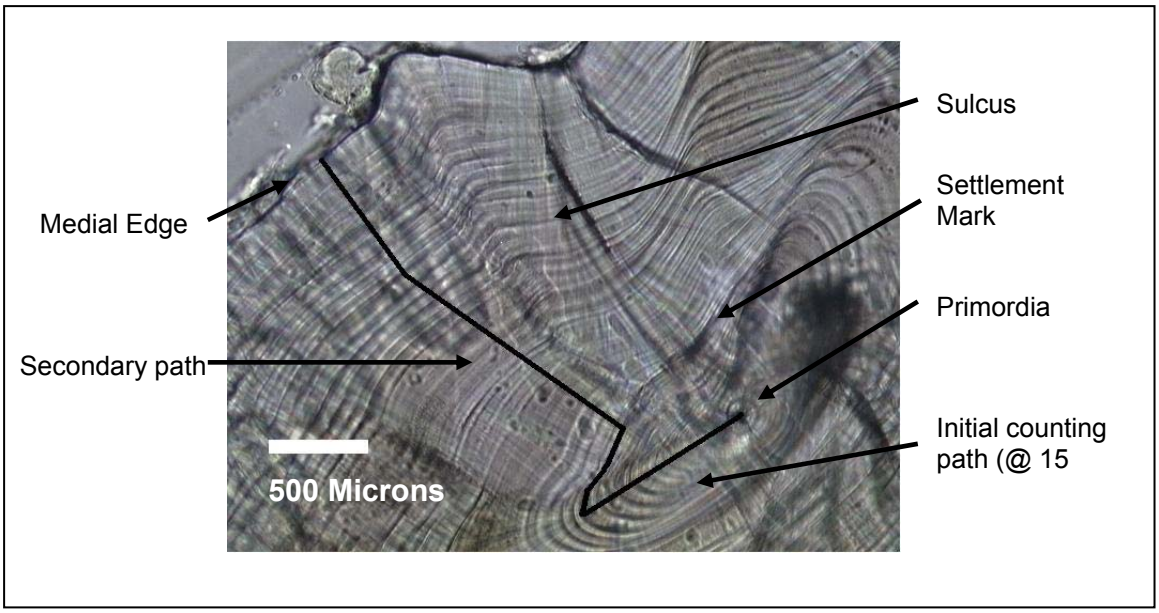

Figure 2. Transverse polished section of sagittal otolith from a 79 d old red drum (37mm TL).

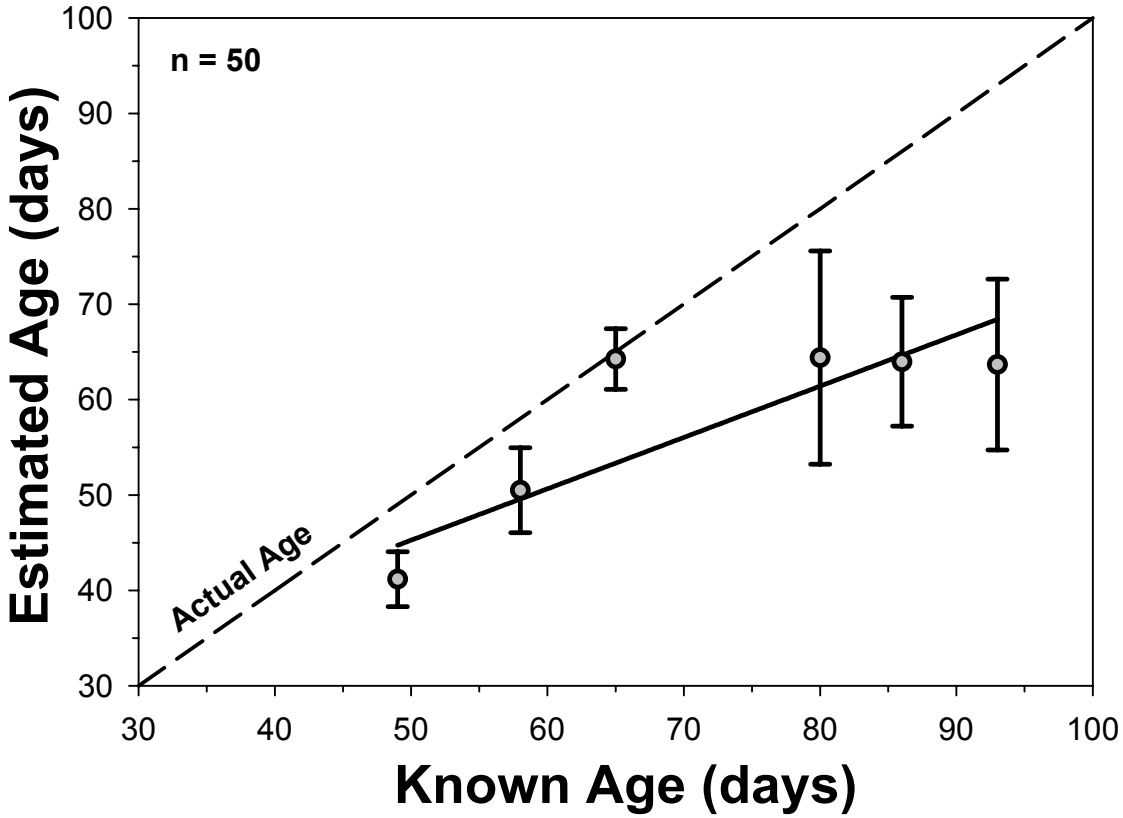

Figure 3. Age bias plot of known age of hatchery-reared fish versus estimated reader age. Each error bar represents the 95% confidence interval for all fish of a specific known age. The dashed line has a slope of 1.

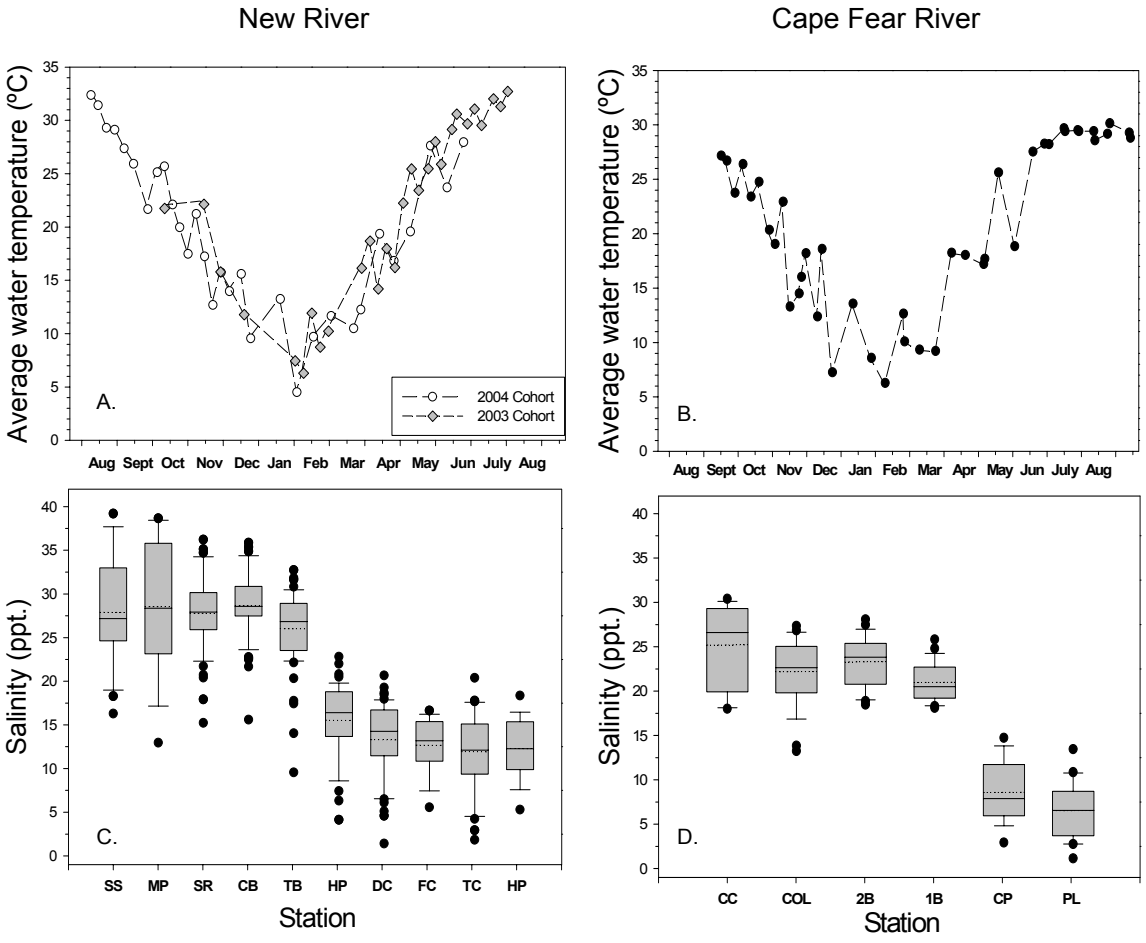

Figure 4. Average estuarine water temperatures (A) and water salinities (C) recorded at sample sites in the New River for the 2003 and 2004 cohorts. Water salinities at each station were pooled together for the 2003 and 2004 cohort in the New River. Average estuarine water temperatures (B) and water salinities (D) recorded at sample sites in the Cape Fear River for the 2004 cohort.

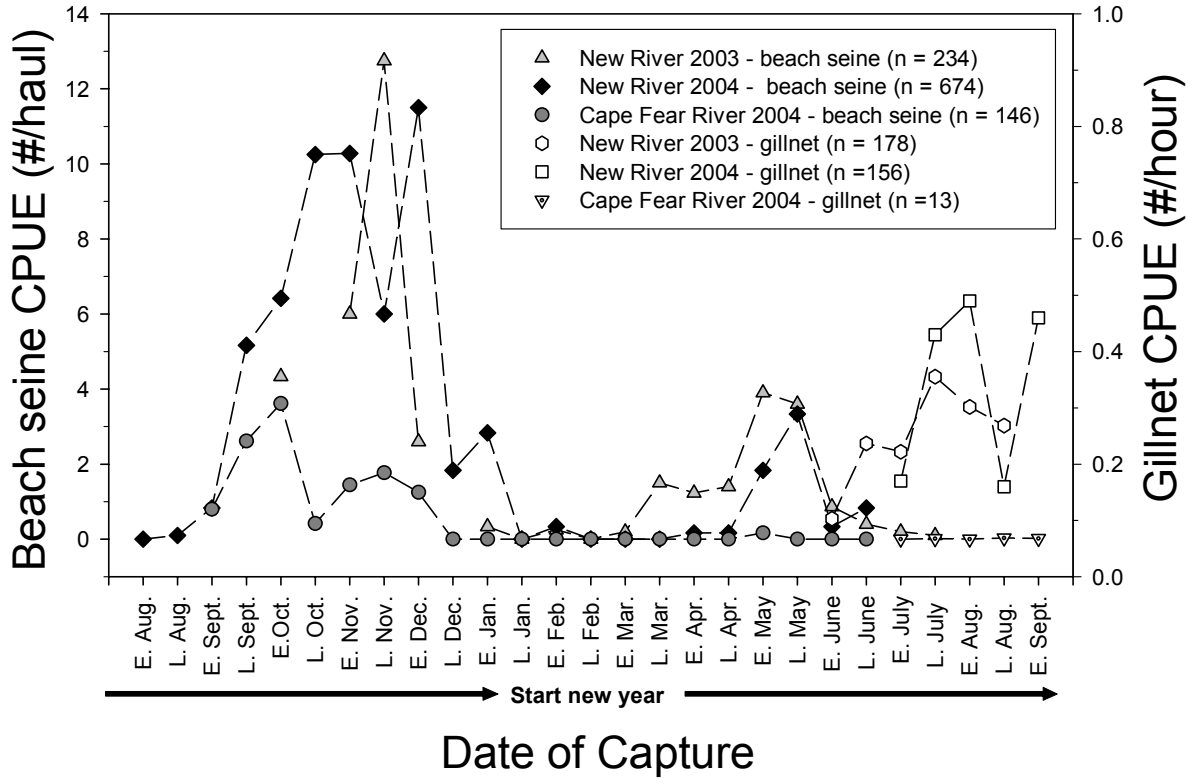

Figure 5. Biweekly beach seine and gillnet catch-per-unit-effort (CPUE) for the 2003 and 2004 red drum cohort during the first year in the New River and the Cape Fear River estuaries.

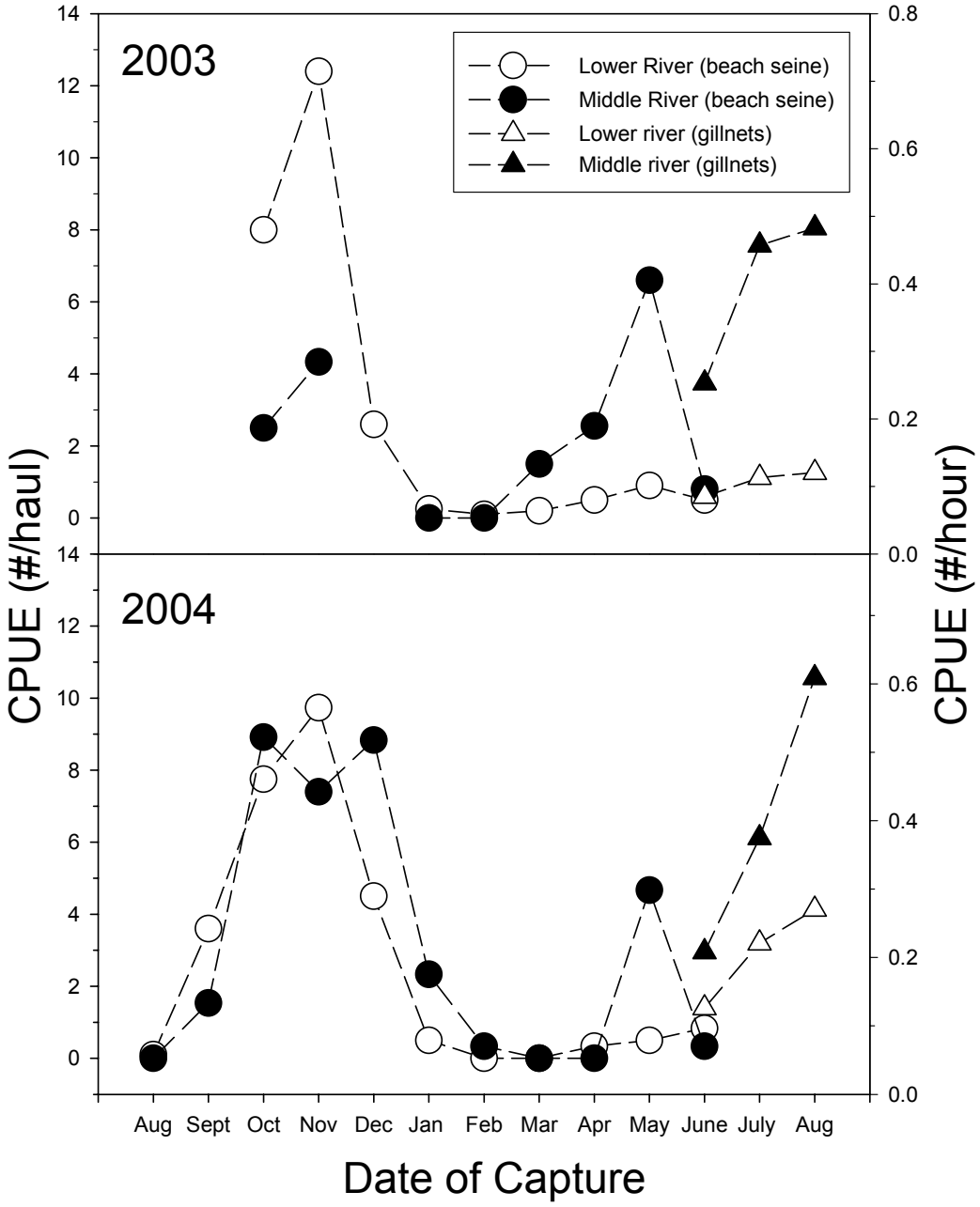

Figure 6. Monthly comparison of seasonal beach seine and gillnet catch-per-unit-effort (CPUE) between lower and middle river locations. Seines conducted August through June; gillnets June through August.

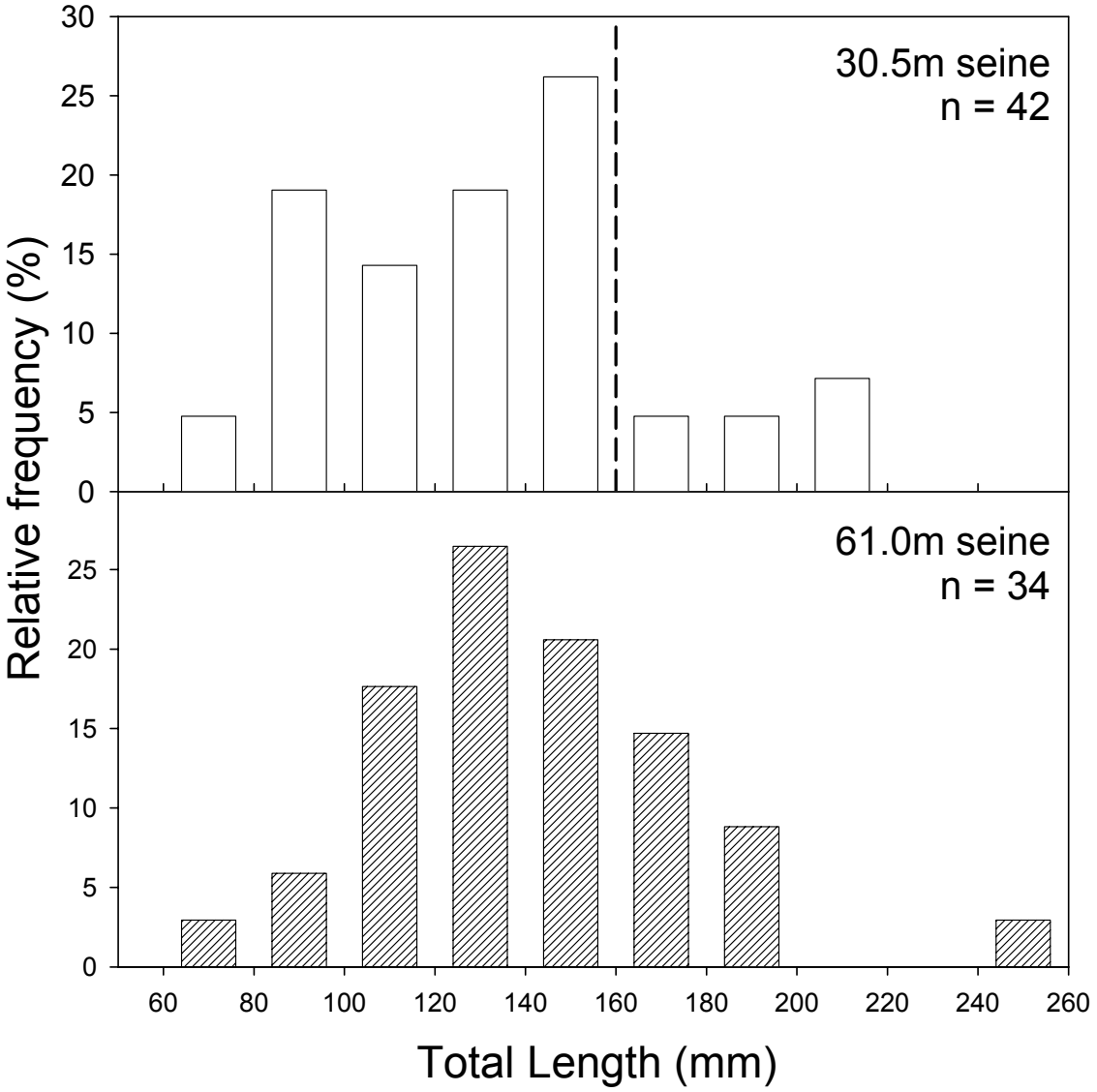

Figure 7. Length-frequency distributions of juvenile age-0 red drum captured in 30.5 and 61.0m beach seines as part of spring 2005 capture efficiency experiment. Dashed line in the upper panel indicates reduce capture efficiency for red drum > 160mm TL in the 30.5m beach seine.

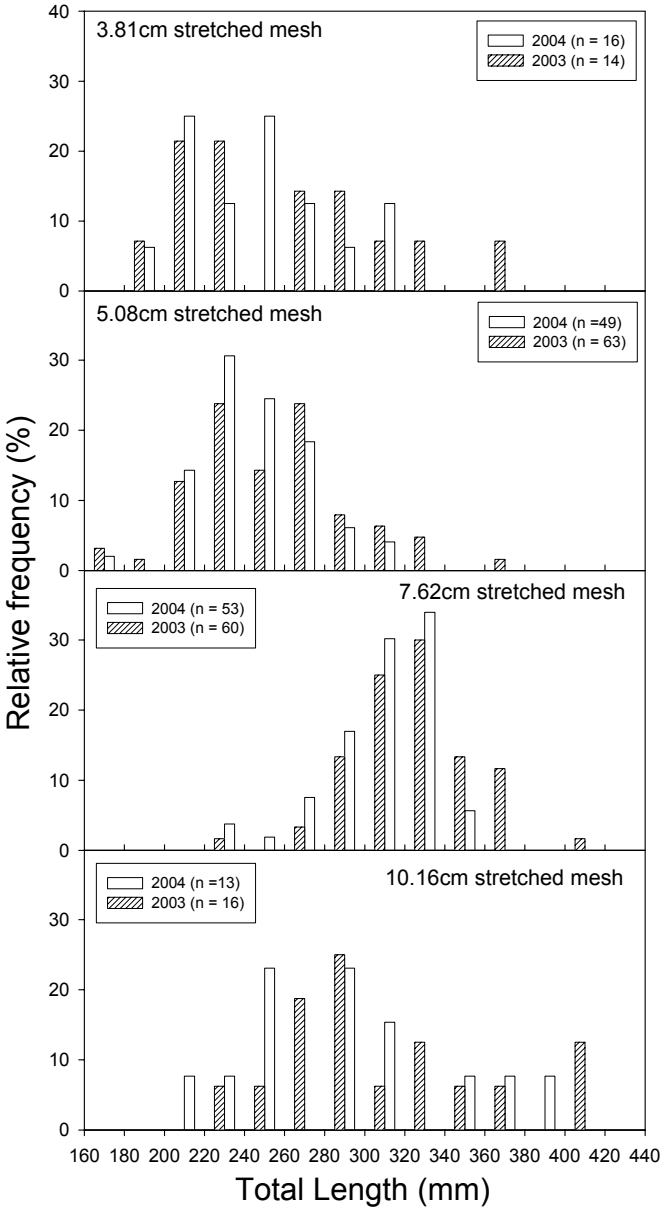

Figure 8. Length-frequency distributions of red drum caught in multi-panel gill nets in the New River during the summers of 2004 and 2005.

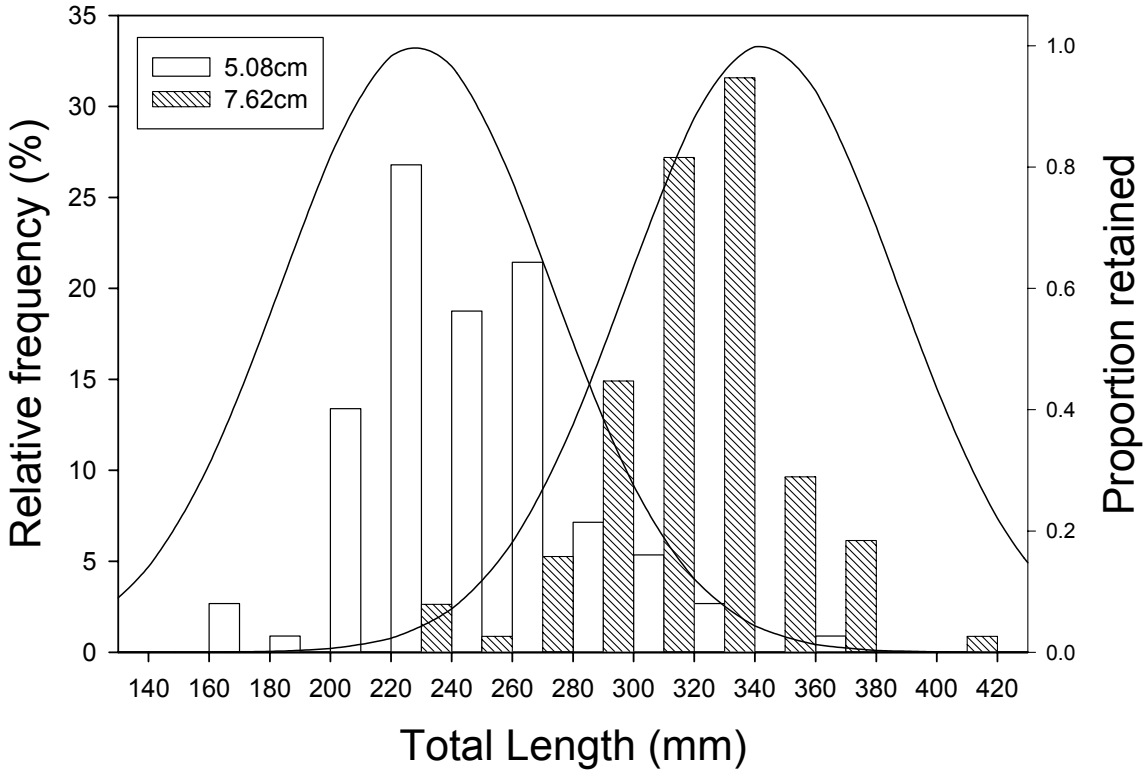

Figure 9. Selection curves for the 5.08 and 7.62cm (stretched) gillnet panels for red drum collected in the New River during the summers of 2004 and 2005.

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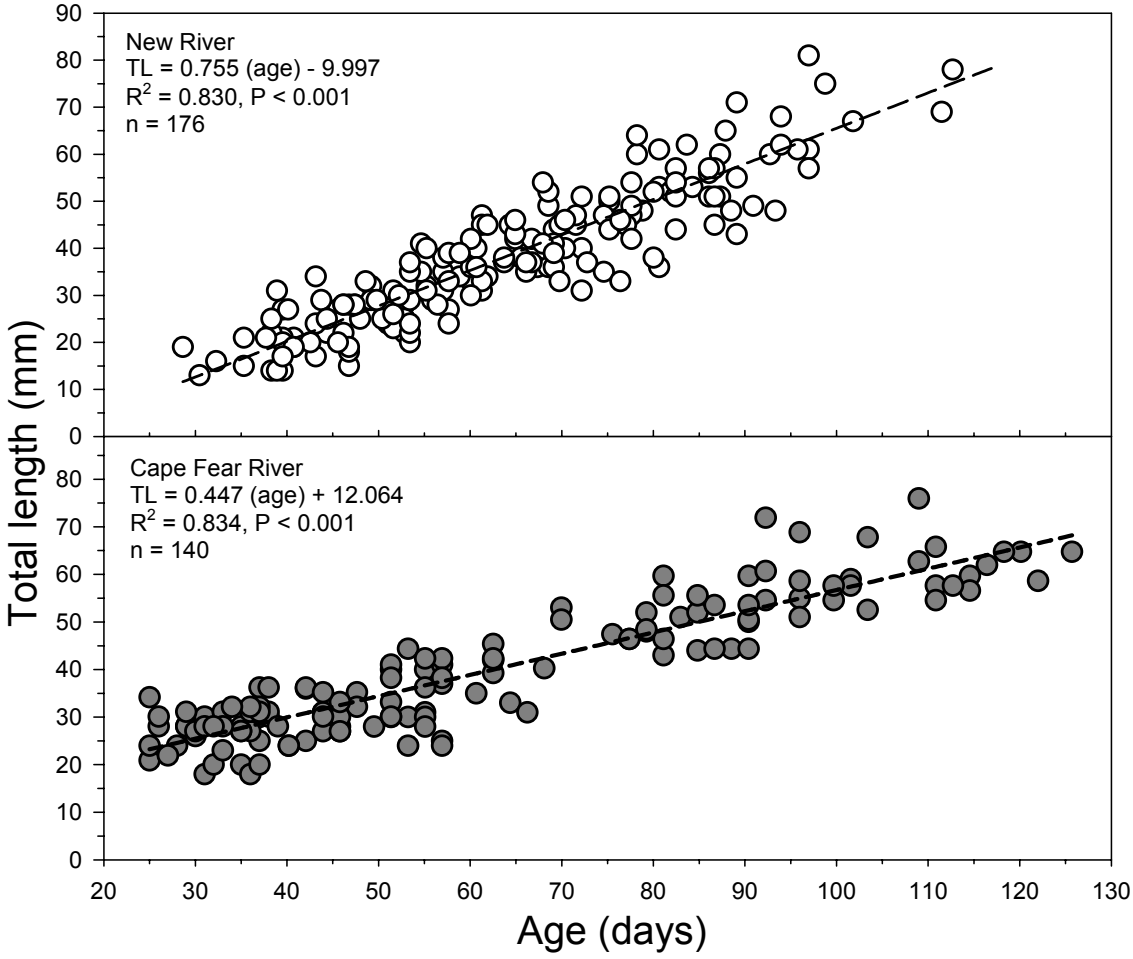

Figure 10. Length-at-age relationships for age-0 red drum juveniles in the New River and Cape Fear estuaries in 2004.

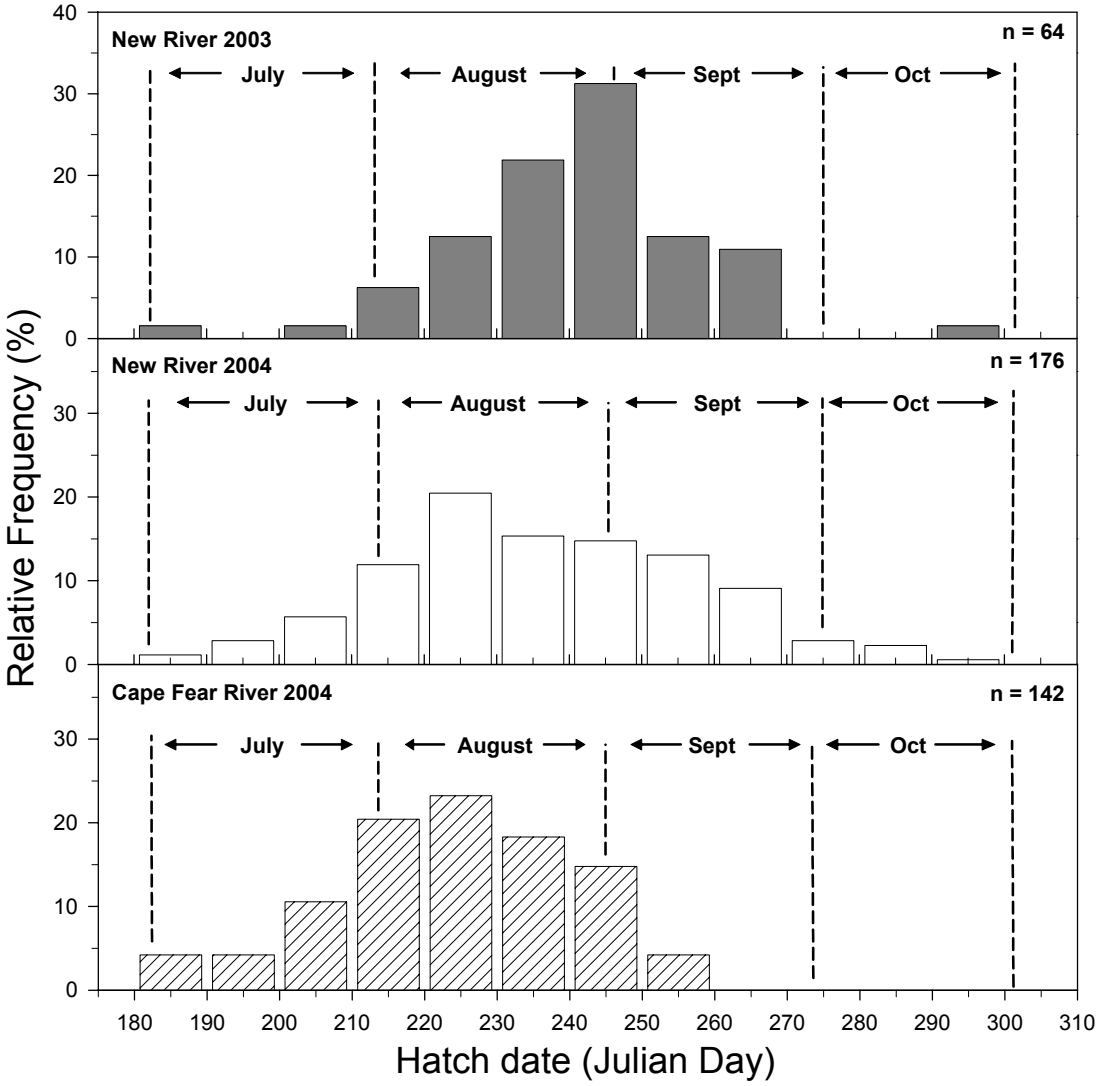

Figure 11. Estimated hatch date distributions for juvenile red drum collected during fall 2003 and 2004 in the New River estuary.

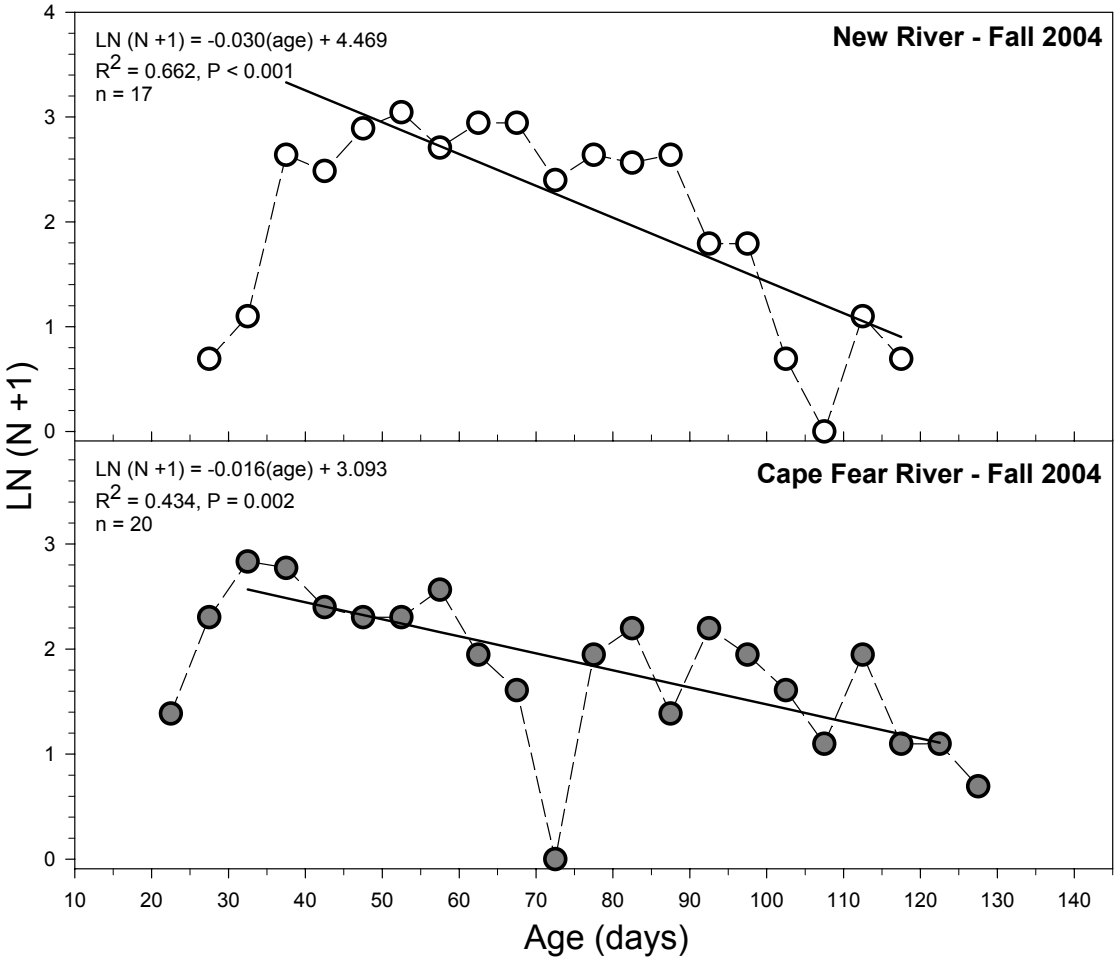

Figure 12. Abundance (LN (N +1)) at age plots for juvenile red drum during fall 2004 in the New River and Cape Fear River estuaries. Regression coefficients represent total instantaneous mortality (Z) or loss rate.

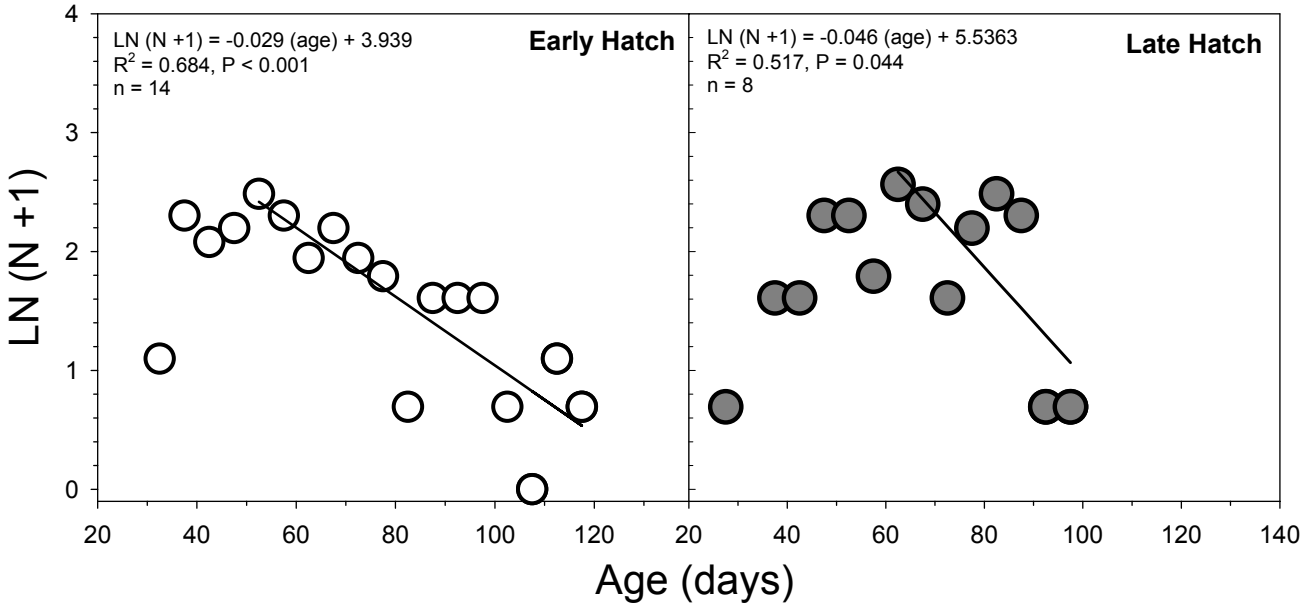

Figure 13. Abundance (LN (N+1)) at age plots for early and late hatched red drum during fall of 2004 in the New River estuary. Regression coefficients represent total instantaneous mortality (Z) or loss rates.

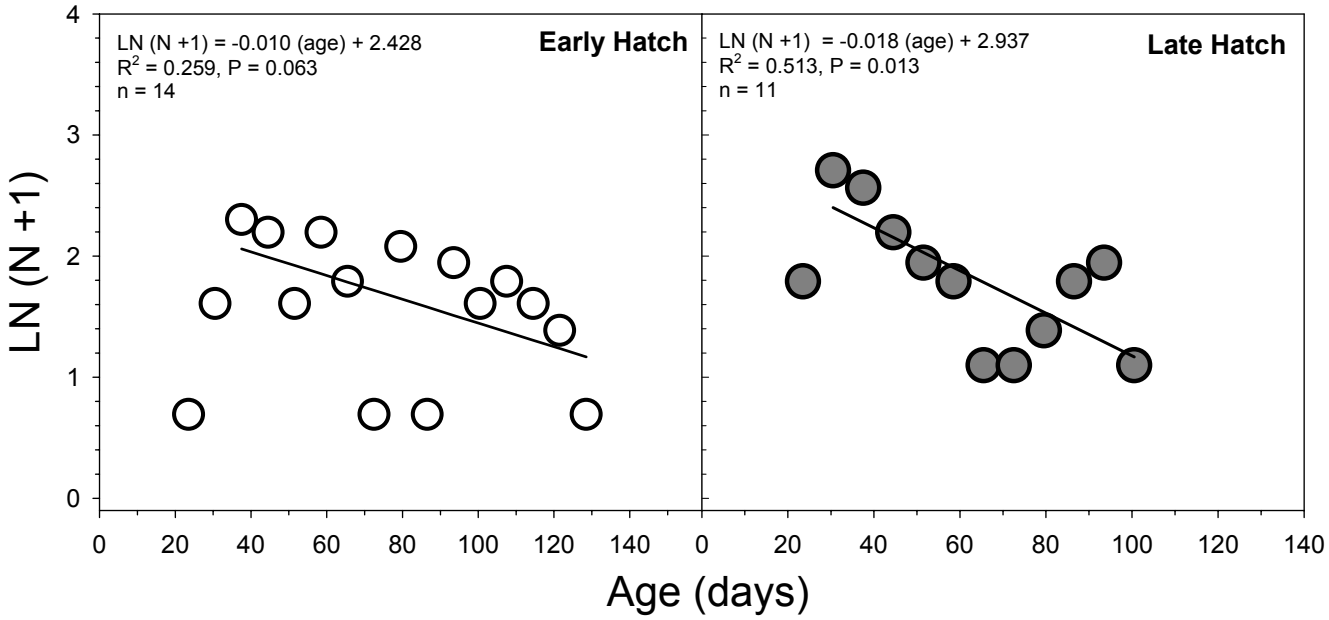

Figure 14. Abundance (LN (N+1)) at age plots for early and late hatched red drum during fall of 2004 in the Cape Fear River estuary. Regression coefficients represent total instantaneous mortality (Z) or loss rates.

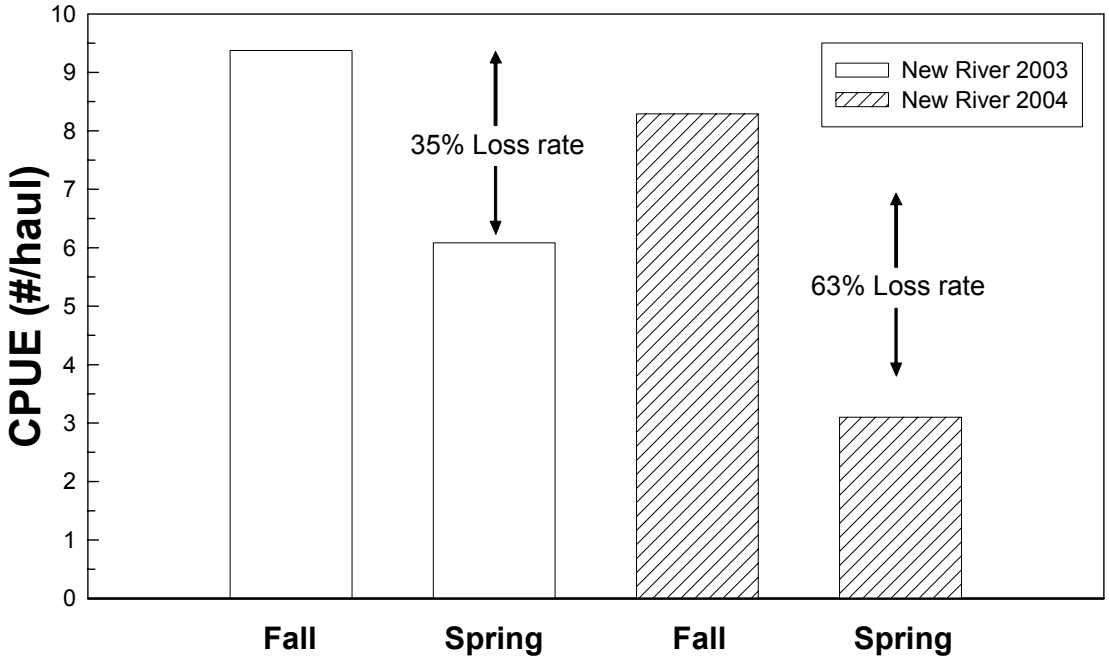

Figure 15. Comparison of seasonal beach seine (30.5m) catch-per-unit-effort (CPUE) between November and May used to estimate overwinter loss rates (mortality + emigration) in the New River in 2003 and 2004.

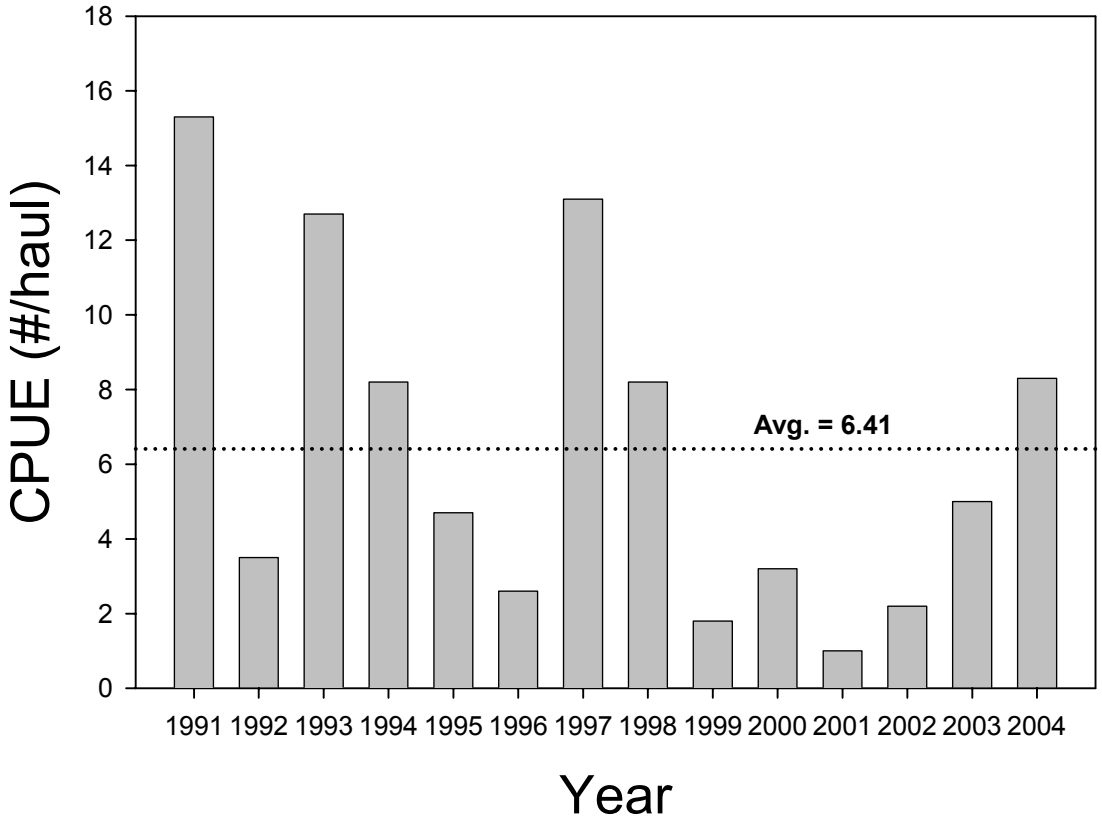

Figure 16. Statewide annual catch-per-unit-effort (CPUE) estimates for age-0 red drum collected as part of the North Carolina Division of Marine Fisheries (NCDMF) Juvenile Abundance Index (JAI).

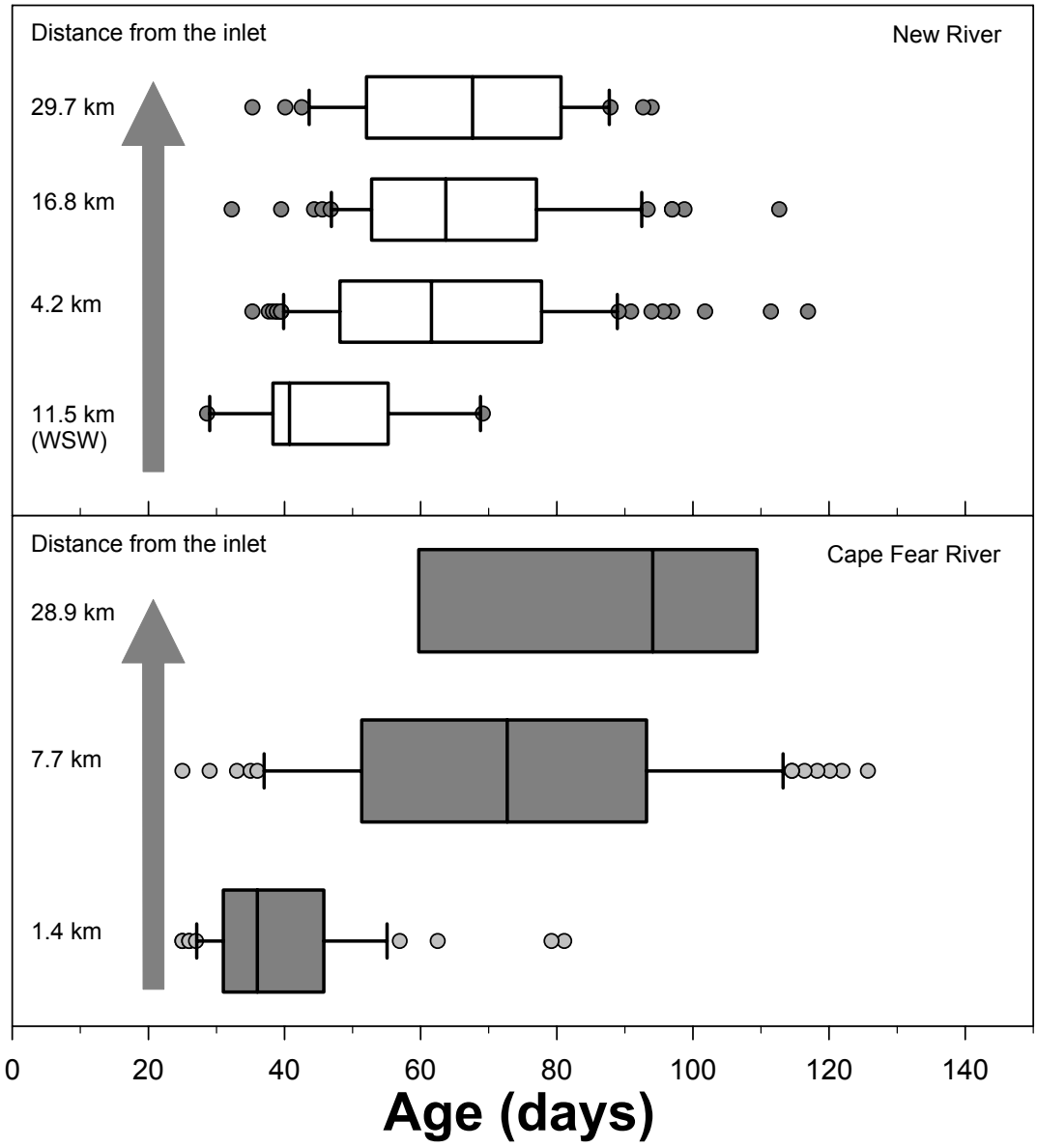

Figure 17. Spatial distributions of older age-0 red drum observed in the Cape Fear River and in New River estuaries indicating habitat shifts from inlet passes to more mesohaline regions as they grew older. Bars within box and whisker plots indicate median age.

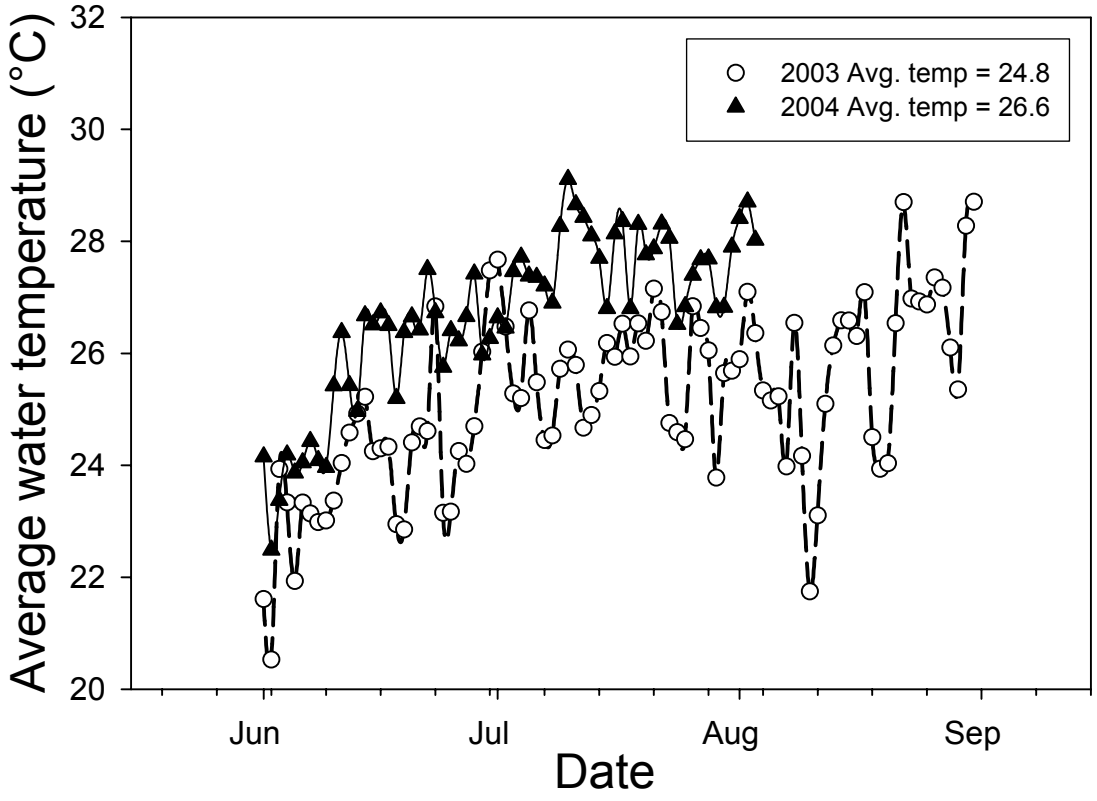

Figure 18. Nearshore summer water temperatures recorded at the Diamond Shoals Buoy (station 41025) located near the Cape Hatteras Inlet, North Carolina (35°00'22" N 75°24'07" W).